

Fire-mediated alternative stable states in the vegetation communities of southwest Tasmania



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Statement of publication

Peer-reviewed publications produced as part of this thesis:

- (1) **Wood, S.W.**, Murphy, B.M., and Bowman, D.M.J.S. (2011) Firescape ecology: how topography determines the contrasting distribution of fire and rainforest in the southwest of the Tasmanian Wilderness World Heritage Area. *Journal of Biogeography*, **38**, 1807-1820.
- (2) **Wood, S.W.** and Bowman, D.M.J.S. (In Press) Alternative stable states and the role of fire-vegetation-soil feedbacks in the temperate wilderness of southwest Tasmania. *Landscape Ecology*, (accepted for publication, October 17, 2011).
- (3) **Wood, S.W.**, Hua, Q. and Bowman, D.M.J.S. (2011) Fire-patterned vegetation and the development of organic soils in the lowland vegetation mosaics of southwest Tasmania, *Australian Journal of Botany*, **59**, 126-136.
- (4) **Wood, S.W.**, Hua, Q., Allen, K.J. and Bowman, D.M.J.S. (2010) Age and growth of a fire prone Tasmanian temperate old-growth forest stand dominated by *Eucalyptus regnans*, the world's tallest angiosperm. *Forest Ecology and Management*, **260**, 438-447.
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Statement of co-authorship

In regards to the above list of peer reviewed publications:

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Abstract

The World Heritage listed landscapes of southwest Tasmania are an ideal model system for investigating the role of fire in shaping the distribution of fire-sensitive and fire-adapted vegetation communities. Two models of vegetation dynamics have been put forward to explain the mosaic of rainforest, sclerophyll and treeless moorland vegetation in this region: the alternative stable states model of Jackson (1968) and the sharpening switch model of Mount (1979). Drawing on the concepts in these models, the aims of this thesis were to (a) contribute new evidence on the decadal, century and millennial scale dynamics of southwest Tasmanian vegetation communities and (b) investigate the role of interactions between fire, vegetation, soil and the physical environment in determining observed vegetation dynamics.

The application of geospatial statistics to mapped distributions of rainforest vegetation and the spatial pattern of four very large fires confirmed that the distribution of fire-sensitive rainforest is related to topographic fire refugia. Topography clearly plays an important role in mediating the feedbacks between fire and vegetation in southwest Tasmania. This study also provided the first integrated data on the relative flammability of the major vegetation communities at the landscape scale.

Repeat image analysis of aerial photographs (1948, 1988) and satellite imagery (2010) revealed that forest and non-forest vegetation communities have been largely stable over the last sixty-two years. Decadal scale fluctuations near forest boundaries were related to recovery from stand replacing fire and the very slow encroachment of trees into moorland. Analyses of soil samples collected across stable forest boundaries suggested that fire-vegetation-soil feedbacks may contribute to the maintenance of vegetation communities over time. Evidence from radiocarbon dating showed that interactions involving soils are also influenced by topography and its effect on drainage. This study also showed that stable

carbon isotopes in organic soil profiles cannot be used to examine millennial scale vegetation boundary shifts in southwest Tasmania.

Dendro-ecology studies revealed that an even-aged cohort of *Eucalyptus regnans* and *Phyllocladus aspleniifolius* established after a stand-replacing fire in 1490-1510AD. Therefore, overstorey *E. regnans* trees can live for well in excess of 500 years. Current models of forest dynamics for southwest Tasmania clearly underestimate the time frame required for century scale transitions from eucalypt forest to rainforest in productive systems.

Whilst there is some evidence to support the alternative stable states model for southwest Tasmanian vegetation communities, this support must remain equivocal. Vegetation patterns in southwest Tasmania appear to be predominantly stable at a range of temporal scales and interactions between fire, vegetation, soil fertility and topography are likely to contribute to the resilience of vegetation communities. Transitions between vegetation types can occur, although the time frames for transitions appear to be underestimated by current models. Further investigations into feedback mechanisms, the role of the physical environment and state-transition dynamics are required. The implementation of a well designed vegetation monitoring system is an important step toward our understanding and management of the relationships between fire and vegetation in southwest Tasmania under current and future climates.

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Chapter 1: Introduction

Introduction

Fire-vegetation interactions in flammable landscapes

In the broadest sense, the distribution of the world's major biomes can be reasonably well predicted from temperature and precipitation. However, ecosystems within many of these biomes may be characterised by a 'fire disclimax', where potential vegetation is displaced by fire adapted vegetation communities as a consequence of the effects of landscape fire. Fire has been present long enough, and over large enough areas, to drive the evolution of distinctive global ecosystems (Bond and Keeley, 2005; Bond *et al.*, 2005; Bowman *et al.*, 2009) and is a key factor in explaining the coexistence of vegetation communities with different tolerance and adaptation to fire at continental (e.g. Sankaran *et al.*, 2005; Lehmann *et al.*, 2011) and regional scales (e.g. Ash, 1988; Geldenhuys, 1994; Kauffman *et al.*, 1994; Perry and Enright, 2002). Fire is particularly pervasive in shaping vegetation patterns in Australia (Bradstock *et al.*, 2002) and has been implicated as the most critical factor controlling the fragmentary distribution of fire-sensitive rainforest within vast tracts of flammable sclerophyll vegetation from the monsoonal north to the temperate south (Bowman, 2000).

Disentangling the relationships between fire and vegetation is a key challenge for researchers and land managers (Bowman *et al.*, 2009). For example, interactions between fire and vegetation have implications for the conservation of biodiversity (Whelan, 1995; Bradstock *et al.*, 2002), carbon cycling (Thonicke *et al.*, 2001; van der Werf *et al.*, 2006) and the management of large, uncontrolled wildfires in the landscape (Westerling *et al.*, 2006; Lohman *et al.*, 2007). However, understanding these relationships is difficult because of the multitude of climatic, environmental and human factors that interact with fire and vegetation

at various spatial and temporal scales (Whelan, 1995; Bond and van Wilgen, 1996). This task is further complicated by the potential effects of anthropogenic climate change on fire regimes and vegetation dynamics (IPCC, 2007).

Ecological models that attempt to capture the true complexity of fire-vegetation dynamics play an important role in improving our understanding of fire-driven ecosystems. These ecological models have progressed from the equilibrium-based succession paradigm (Clements, 1916) to models of non-equilibrium dynamics that emphasise the effect of disturbance in structuring ecosystems at multiple spatial and temporal scales (Perry, 2002). Assessment of the efficacy of these models requires testing of their underlying assumptions in real-world landscapes (Bowman and Murphy, 2011). For example, savanna ecosystems have provided an ideal ‘model landscape’ to explore how fire-vegetation interactions affect the coexistence of tree and grass vegetation communities across large climatic gradients (Sankaran *et al.*, 2005; Lehmann *et al.*, 2011).

Southwest Tasmania: a model landscape for exploring fire-vegetation interactions

One of the archetypal examples of a vegetation mosaic that has been shaped by fire exists in the southwest of Australia’s largest island, Tasmania (Figure 1.1). Southwest Tasmania is a mountainous and perennially wet region of high conservation value that forms a large part of the Tasmanian Wilderness World Heritage Area. The lowland (*ca.* < 900m a.s.l.) vegetation mosaic of the region is central to the outstanding natural and cultural values that contribute to its World Heritage listing. In southwest Tasmania, fire-sensitive rainforests persist as fragmented pockets within a mosaic of flammable vegetation that is dominated by vast tracts of treeless moorlands, but also includes a range of sclerophyll scrub and forest communities. The cool temperate rainforests are a relictual stronghold of an ancient Gondwanan flora that

once covered the Australian continent. The highly flammable moorland vegetation is dominated by Buttongrass (*Gymnoschoenus sphaerocephalus*). The region is comprised largely of nutrient-poor quartzitic bedrock and is blanketed by highly acidic organic soils that are unique to the Australian continent. The most nutrient rich areas in sheltered valleys give rise to the tallest flowering plants in the world, *Eucalyptus regnans*, which can grow to approximately 100 meters and form some of the most carbon dense forests in the world (Dean *et al.*, 2004; Keith *et al.*, 2009).

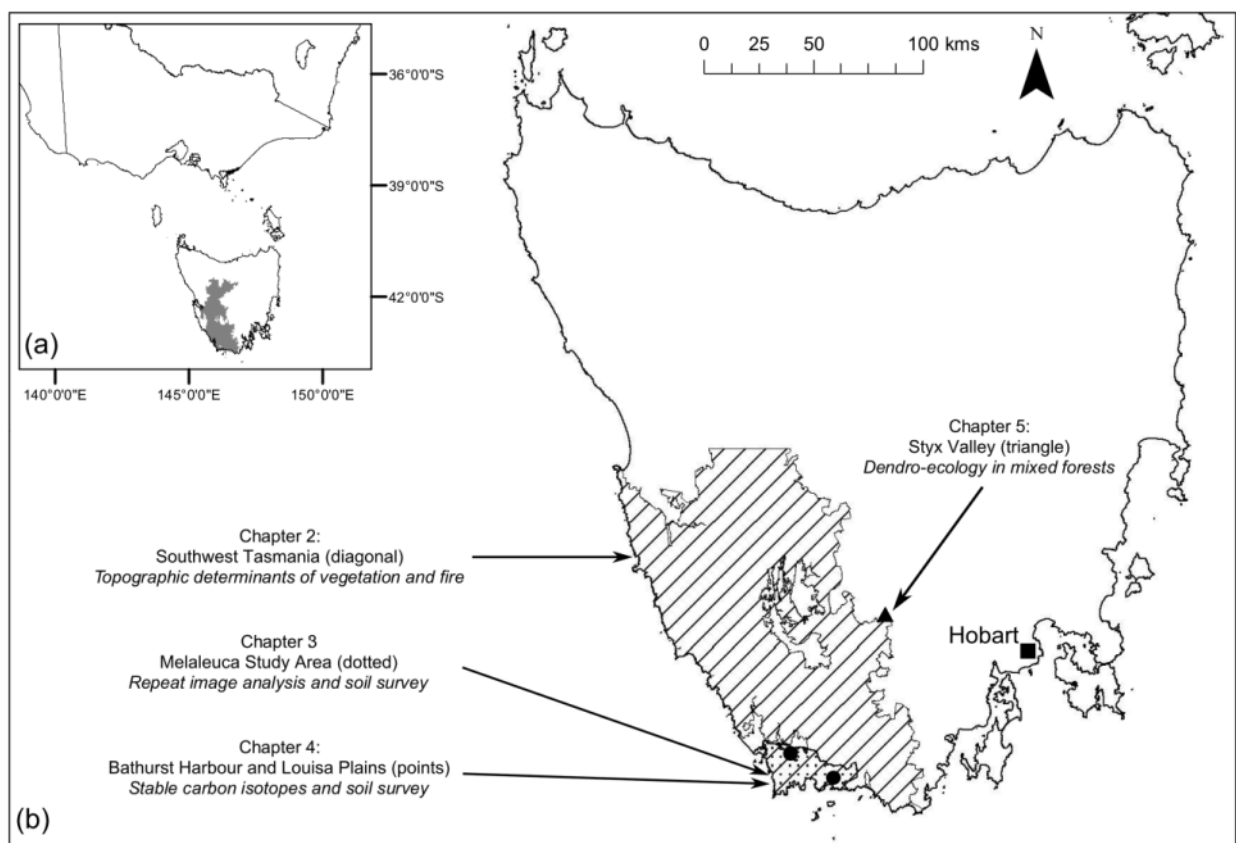


Figure 1.1. (a) location of the island state of Tasmania in southeast Australia and the extent of the Tasmanian Wilderness World Heritage Area (grey shading). (b) The geographic location of four studies undertaken in southwest Tasmania at regional (Chapter 2), landscape (Chapter 3) and local scales (Chapters 4 and 5).

It has long been recognised that fire has been central to shaping the vegetation mosaic of southwest Tasmania (Gilbert, 1959; Jackson, 1968) and that landscape burning by humans has profoundly influenced the evolution of these vegetation patterns (Jackson, 1999; Marsden Smedley and Kirkpatrick, 2000). Indeed, it has been argued that southwest Tasmania represents an ‘ancient cultural landscape’ (Fletcher and Thomas, 2010a). Aboriginal occupation of southwest Tasmania stretches back to 35,000 years BP and, given the rarity of lightning strikes, humans were probably the primary source of ignitions in this region (Bowman and Brown, 1986). European colonisation caused the expatriation of the Aboriginal tribes in the mid 1800’s. This led to a shift in the fire regimes of southwest Tasmania to intense, infrequent fires until the 1940’s, followed by fire suppression and strategic prescription burns (Marsden-Smedley, 1998).

The southwest Tasmanian landscape is a model landscape for exploring the relationships between fire and vegetation and their interaction with humans, climate and the physical environment (i.e. topography, soils, geology). As a World Heritage Area there is a clear imperative to understand the nature of vegetation dynamics to inform the management of the regions’ natural and cultural values (Brown, 1996; Marsden Smedley and Kirkpatrick, 2000). Two models have been put forward to explain these vegetation dynamics: the ‘alternative stable states’ or ‘ecological drift’ model of Jackson (1968) and the ‘sharpening switch’ or ‘stable fire cycles’ model of Mount (1979).

Jackson’s alternative stable states model

Jackson’s (1968) so-called ‘ecological drift’ model sought to answer a deceptively simple question: given that the climatic and edaphic characteristics of southwest Tasmania are suitable for the widespread dominance of temperate rainforest, why should this vegetation

type be spatially restricted to fragmented pockets in a matrix of sclerophyll vegetation? Jackson argued that this decoupling of vegetation from the prevailing climate was due to complex interrelationships between vegetation, fire, soil fertility and humans (Figure 1.2). Jackson identified six vegetation communities – moorland, moorland-heath, wet scrub, wet sclerophyll forest, mixed eucalypt-rainforest and rainforest. Each vegetation community actively modifies the rate of fuel accumulation and fuel characteristics (i.e. fire frequency, Figure 1.3), soil nutrient capital and light environment in a direction that enhances its own growth and survival, and simultaneously hinders or constrains other vegetation types. Jackson (1968; 2000) suggested that these positive feedbacks between fire, vegetation and soil collectively encourage an inherent resilience to change in each of the southwest Tasmanian vegetation communities. Importantly, Jackson (1968) included the possibility that chance deviations in fire frequencies – assumed to be highly improbable – could cause the transition of one stable vegetation community to another along a range of pathways (Bowman and Jackson, 1981; Figure 1.3). Jackson (1968) proposed a negative binomial distribution for the probability of fire in forest communities (Figure 1.3), thus allowing for the high flammability of recently burnt forest vegetation and the higher likelihood of vegetation transitions during this period. Jackson believed that humans living in the landscape were the primary source of ignitions.

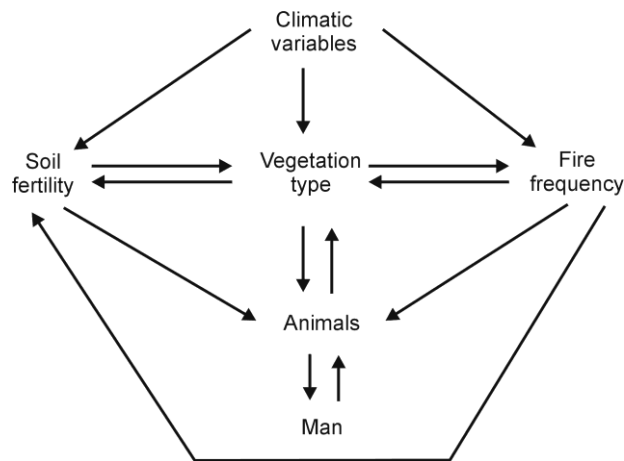


Figure 1.2. Hypothesised ecological interactions that determine vegetation types in southwest Tasmania.

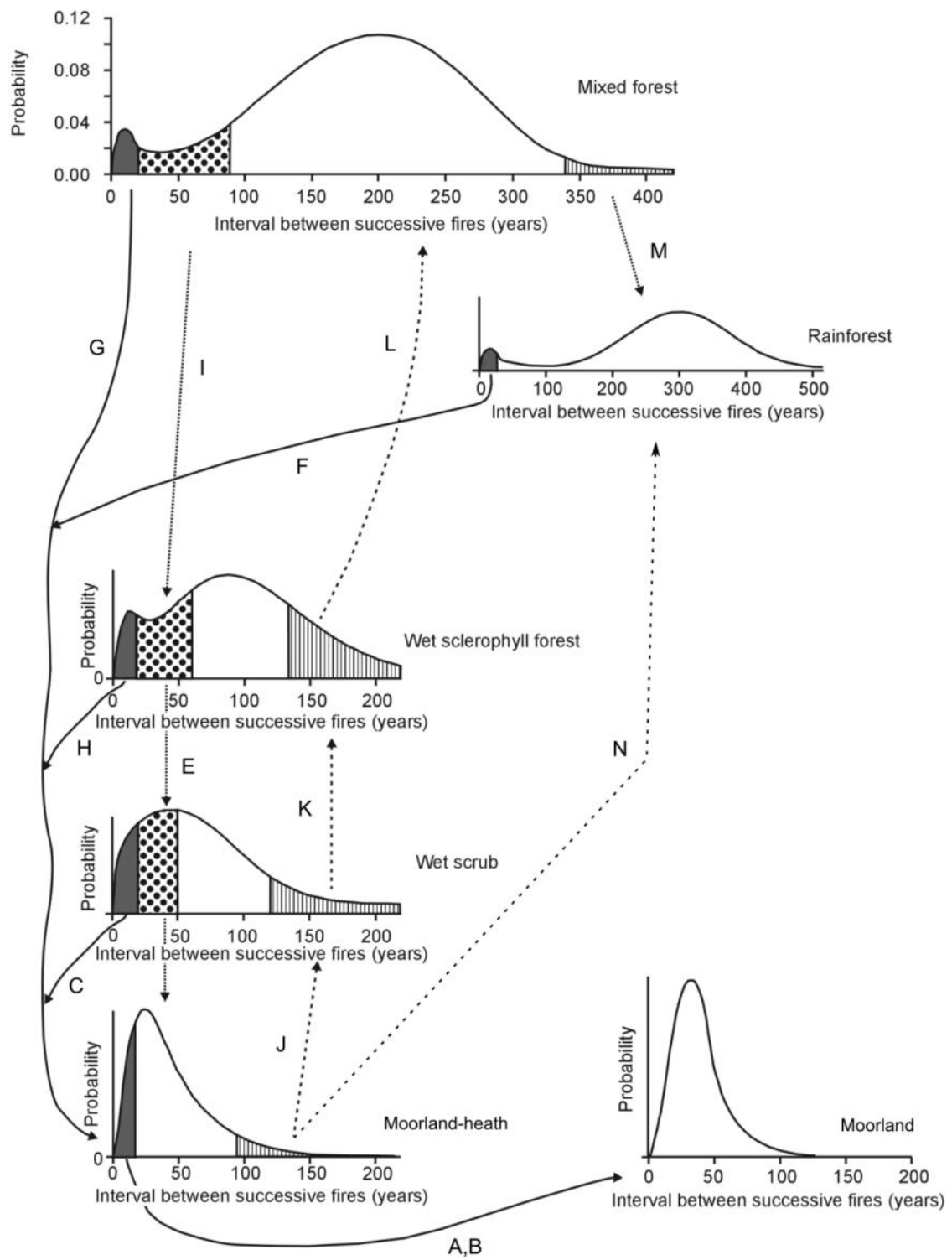
Figure 1.3. (adjacent) Jackson's (1968) model of 'ecological drift' for six vegetation communities in southwest Tasmania. The diagram shows probability distributions for fire-free intervals in each vegetation type. Transitions from one vegetation type to another are governed by fire-free intervals that arise due to chance. The letters identify each possible transition and correspond to those used in Bowman and Jackson (1981).

Solid arrows describe the replacement of woody vegetation types with non-forest vegetation. Such transitions occur when two fires occur in quick succession, killing regenerating woody plants before they are sexually mature. The probability of these 'stand replacing' fires happening is shown as black shading.

Dotted arrows described the replacement of mixed *Eucalyptus-Nothofagus* forest by wet sclerophyll forest, wet sclerophyll forest by wet scrub and wet scrub by sedge-heath. These transitions occur because the interval between two successive fires is insufficiently long to allow the sexual maturity of the dominant plants in vegetation (e.g. *Eucalyptus* in wet sclerophyll forests) but sufficiently long for the maturity of plants in the previous stage (e.g. *Melaleuca* in wet scrub). The probability of this happening is shown in hatched shading.

Dashed arrows describe the replacement of sedge-heath by wet scrub, wet scrub by wet sclerophyll forest, wet sclerophyll forest by mixed *Eucalyptus-Nothofagus* forest and mixed *Eucalyptus-Nothofagus* forest by rainforest. These transitions occur because the interval between two successive fires is sufficiently long to allow the establishment and sexual maturity of the long-lived plants that would otherwise be eliminated by shorter fire-free intervals. The probability of this happening is shown in by dotted shading.

Unshaded areas of each graph denote fire-free interval that would maintain each of the given vegetation types.



The model Jackson proposed is effectively an alternative stable states model. Indeed, Jackson's model is one of the earliest alternative stable states models for fire driven landscapes in the literature (see also Mutch, 1970). Models of alternative stable states are often used to explain why assemblages of different vegetation communities can occur side by side in the same environment (Scheffer *et al.*, 2001; Scheffer and Carpenter, 2003). Each state is controlled by a set of stabilising feedback processes that act to maintain that state (Wilson and Agnew, 1992; Folke *et al.*, 2004). Transitions among otherwise stable states occur when feedbacks break down or when environmental changes exceed thresholds. These transitions are often rapid and may not be reversible on short time scales (Scheffer *et al.*, 2001). There has been a recent surge of interest in alternative stable states theory and its role in explaining the juxtaposition of flammable and fire-sensitive communities in landscapes that experience periodic fire (Perry and Enright, 2002; Jasinski and Payette, 2005; Beckage and Ellingwood, 2008; Hoffmann *et al.*, 2009; Warman and Moles, 2009; Murphy *et al.*, 2010; Lehmann *et al.*, 2011; Nicholas *et al.*, 2011; Staver *et al.*, 2011). Jackson's model has been cited as a key example in many of these studies (Wilson and Agnew, 1992; Petraitis and Latham, 1999; Latham, 2003; Odion *et al.*, 2010a; Raffaele *et al.*, 2011).

Alternative stable states models are traditionally represented as basins of attraction, illustrated as dips or valleys in a two or three dimensional 'stability landscape' (Scheffer *et al.*, 2001). External drivers and internal feedbacks contribute to shaping each valley and maintaining or shifting the ecosystem configuration from one basin of attraction to another (Warman and Moles, 2009). The Jackson model can be represented in the typical two dimensional schematic (Figure 1.4a), however a three dimensional topographic surface (Figure 1.4d: e.g. Beisner *et al.*, 2003) allows a better representation of the range of possible transition pathways between vegetation states. In alternative stable states parlance (*sensu* Scheffer *et al.*, 2001; Warman and Moles, 2009), the vegetation communities put forward by Jackson

comprise distinct basins of attraction and the strength of the feedbacks between fire, vegetation and soil (Figure 1.4c) determine the depth and size of these basins. Deviations in fire frequencies (e.g. two intense stand replacing fires) are analogous to external perturbations that overwhelm internal feedbacks and push a vegetation community beyond its resilience threshold, causing a transition to a neighbouring basin along a range of pathways. Jackson inferred that more than one stable state is possible for a given set of environmental conditions in the opening line of his paper: ‘there would appear to be no aspect, soil-type or edaphic situation which cannot be occupied by cold temperate rainforest’.

In the absence of robust data on the relative strength of the various feedbacks (particularly for the effect of complex feedbacks with soil nutrients; Jackson, 2000), the topologies of the heuristic diagrams put forward here (Figure 1.4a,d) are only indicative of the dynamics inferred by Jackson (1968). Other interpretations are possible. In this representation, moorland and rainforest communities have deep basins and are highly resilient to change – rainforest rarely burns and non-forest communities rarely transition to forest. Conversely, mixed-forest and scrub are only moderately resilient and can easily slide into neighbouring basins of attraction. Indeed, mixed eucalypt-rainforest may be better represented as an unstable ‘ridge’ rather than a meta-stable ‘basin’ (i.e. Warman and Moles, 2009). The topology of the ‘stability landscape’ slopes downwards from rainforest to non-forest, representing the scenario where the depletion of soil nutrients by repeated fire slows transitions toward rainforest, compared with transitions away from rainforest.

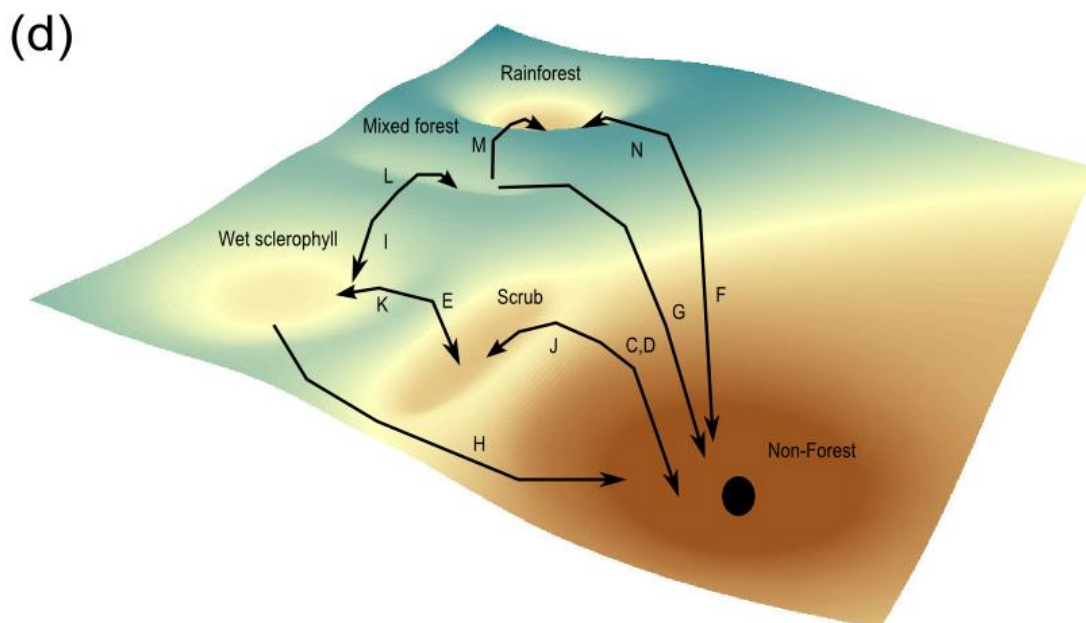
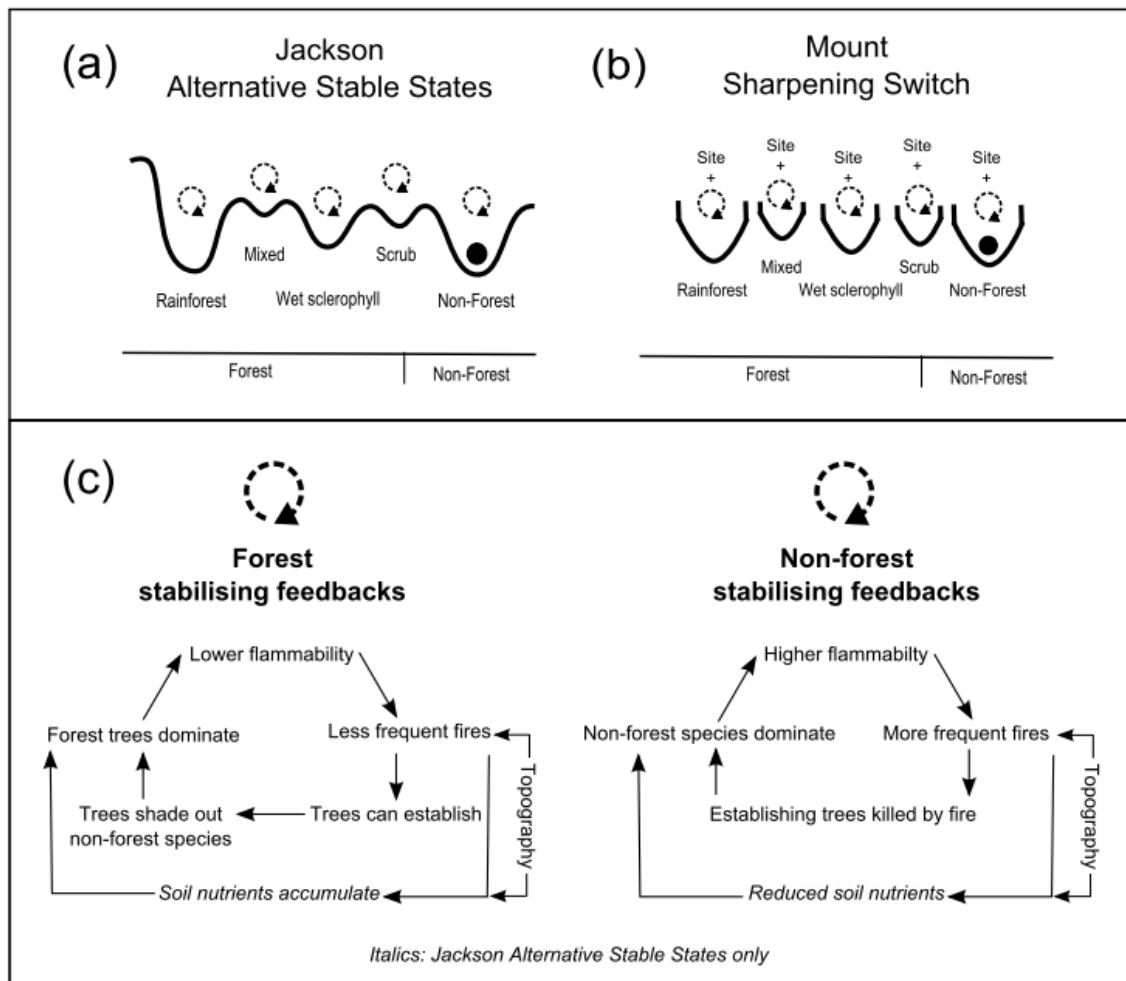
Figure 1.4: Models of vegetation dynamics for southwest Tasmania illustrated with the ‘ball and cup’ heuristic model commonly used to describe alternative stable states (see Scheffer *et al.*, 2001; Warman and Moles, 2009).

(a) In Jackson’s (1968) ‘alternative stable states’ model each vegetation community can occupy any underlying physical environmental setting. Each potential vegetation state is determined by fire-vegetation-soil feedbacks [see (c)] and the cumulative effect of these feedbacks is represented by resilient ‘basins of attraction’. A vegetation community - represented by the ball – will resist disturbance by fire initially and return to the original state, but if pushed beyond the threshold by repeated stand replacing fire (or lack thereof), positive feedbacks from the neighbouring stable state will take over and the system will undergo a transition to another stable state.

(b) In Mount’s (1979) ‘sharpening switch’ model each vegetation community is initially determined by the underlying physical environment (or ‘site’, *sensu* Mount 1979). Feedback mechanisms between fire and vegetation [see (c)] reinforce these patterns by creating deeper ‘basins of attraction’. The resilience created by these feedbacks is strong enough to prevent vegetation state transitions creating stable vegetation patterns.

(c) Conceptual model showing the stabilising feedbacks that maintain the forest and non-forest vegetation states investigated in this study. Adapted from Petraitis and Latham (1999).

(d) An interpretation of the alternative stable states model of Jackson (1968) with five stable states illustrated in three dimensions. The dynamics here are the same as (a) except that transitions can follow multiple pathways between states (i.e. Bowman and Jackson, 1981). The pathways (arrows and labels C-N) correspond to those outlined by Bowman and Jackson (1981) and Figure 1.3. In this representation, non-forest vegetation is shown to be highly resilient due to high fire frequencies and the consequent depletion of nutrients (see text).



The influence of Jackson's model is not limited to alternative stable states. Jackson (1968) has provided a foundational conceptual framework for studies on the effects of fire regimes on landscape scale vegetation dynamics (reviewed by Bowman and Wood, 2009), including (i) the existence of fire regimes that are characteristic of specific vegetation communities (Whelan, 1995; Gill and Allan, 2008); (ii) the millennial scale dynamics of vegetation communities (Macphail, 1984; Singh and Geissler, 1985; Colhoun, 2000); (iii) the interplay between life history attributes, vegetative recovery mechanisms, and recurrent fire disturbance (Noble and Slatyer, 1980; Moore and Noble, 1990); (iv) the decoupling of vegetation patterns from climate by fire (Whittaker and Levin, 1977; Bowman, 2000); (v) the importance of feedbacks between fire frequency and vegetation distributions (Wilson and Agnew, 1992; Odion *et al.*, 2010b); (vi) the effect of fire and vegetation on pedogenesis (Mcintosh *et al.*, 2005; Read *et al.*, 2006); (vii) the evolution of flammability (Bond and Midgley, 1995; McCarthy *et al.*, 2001); and (viii) the impact of prehistoric people on vegetation in the contemporary landscape (Bowman, 1998; Fletcher and Thomas, 2010a). That Jackson's paper is cited in ~140 peer reviewed journal articles from a diverse range of disciplines from Tasmania, across Australia and the world (Figure 1.5), despite appearing in an obscure Australian conference proceedings, is testimony to the global intellectual impact of this theory.

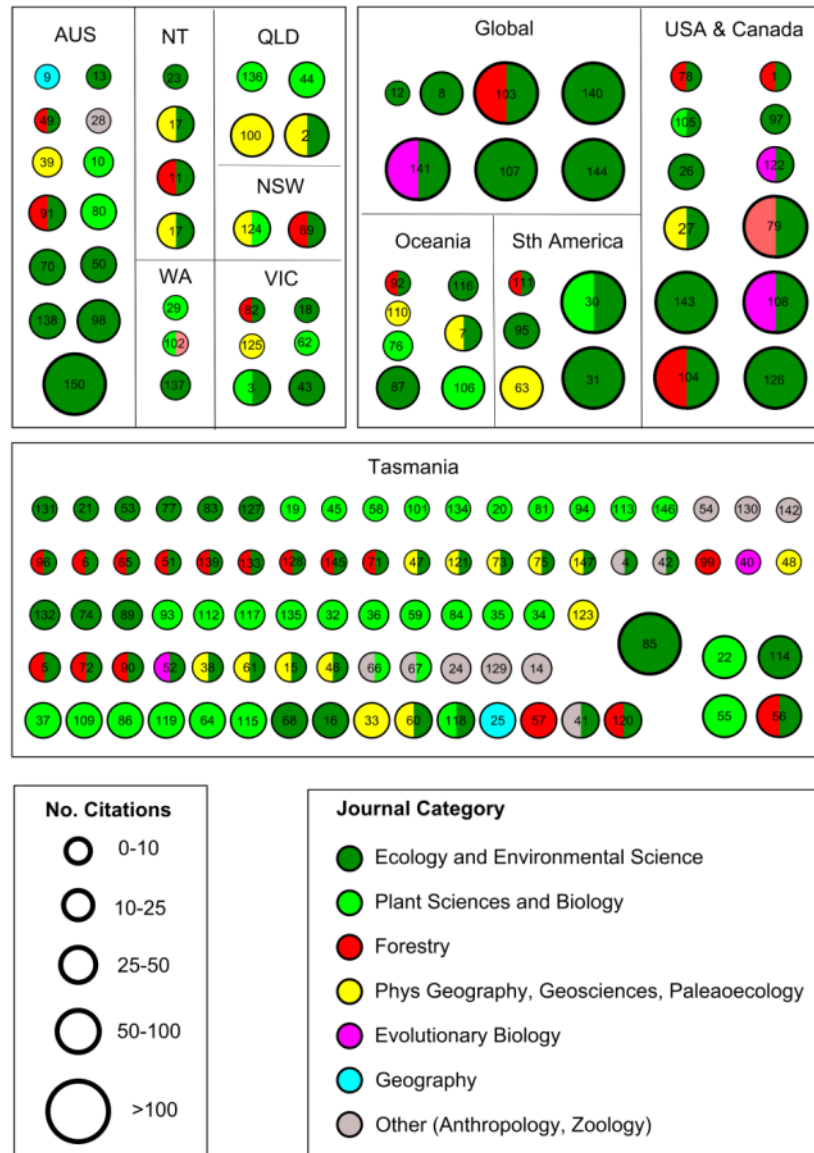


Figure 1.5. The global reach of the Jackson (1968) model. Each numbered circle represents a published paper citing Jackson (1968). Only peer reviewed papers are included. The colour of the circle indicates the subject category of the publishing journal (categories from Web of Science). The size of the circle indicates the number of citations (according to Google Scholar). For example, paper 31 (Cochrane and Laurence, 2002), cited Jackson (1968) as an example of a fire-vegetation feedbacks model. This particular study was conducted in South America, was published in the journal Ecology (ecology and environmental science) and has been cited 163 times. A citation list can be found in Appendix 1.

Mount's sharpening switch model

Mount (1979; see also Mount, 1982) proposed an alternative model to Jackson's that underscores the importance of site characteristics and predicts geographically static vegetation patterns through time. While Jackson allowed for vegetation state transitions, Mount's (1979) so-called 'stable fire cycles' model suggests that the positive feedbacks between fire and vegetation are strong enough to eliminate vegetation state transitions and that physical environmental factors exert significant control over vegetation patterns (Figure 1.4b). Accordingly, fire does not determine vegetation; rather the risk of fire is determined by vegetation, which in turn, is related to 'site factors' in the landscape (i.e. geology, soil fertility, drainage, aspect and topography). For example, rainforest would occur on fertile, well drained soils in fire protected areas and rarely burn, whereas moorland would occur on infertile, poorly drained soils and burn frequently. This model is effectively a 'one-factor sharpening switch' (*sensu* Wilson and Agnew, 1992), where fire merely reinforces environmentally determined vegetation patterns.

Mount did not formalise the specifics of his model in the same detail as Jackson, making direct comparisons difficult. Mount (1979) proposed that the flammability of the dominant species, fuel accumulation rates, and periods of low fuel characteristic of each vegetation type result in highly conserved fire frequencies specific to each vegetation type. In contrast with Jackson (1968), Mount proposed that for a period after each fire event, fuel loads in each vegetation type are too low to maintain a second fire thus preventing transitions toward non-forest. When adequate fuel is present, a fire will burn, thus resetting the 'fire cycle clock' and preventing transitions toward rainforest. Mount noted that the low fuel period during which a community cannot catch fire was estimated to vary from about six months in moorland communities to about 90 years in *Nothofagus* temperate rainforest.

Testing the models: time and space in southwest Tasmania

Assessing the efficacy of alternative stable states models in general requires demonstrating that a state is self sustaining for more than one generation via positive feedback loops (the problem of maintenance) and that pulse events can initiate the development of alternative states (the problem of origin) (Petraitis and Latham, 1999; see also Connell and Sousa, 1983; Peterson, 1984; Sousa and Connell, 1985). Fulfilling these criteria, and distinguishing between the Jackson and Mount models, clearly requires (a) landscape-scale historical ecology studies (Egan and Howell, 2001; Bowman, 2002) that can detect vegetation change (or lack thereof) and (b) targeted studies of fire-vegetation-soil feedbacks and the effect of the physical environment on these feedbacks.

There has been widespread support for Jackson's alternative stable states model for southwest Tasmania (see reviews by Brown and Podger, 1982a; Jackson and Brown, 1999; Bowman, 2000; Jackson, 2000; Bowman and Wood, 2009; Macphail, 2010; Thomas *et al.*, 2010) and various simulation models based on Jackson (1968) have generated realistic predictions of broad vegetation patterns in the current landscape (Henderson and Wilkins, 1975; Brown and Podger, 1982b; King, 2004; King *et al.*, 2006; King *et al.*, 2008). However, the evidentiary basis for such strong support of the Jackson model is surprisingly limited for southwest Tasmania, with few field studies able to adequately capture the spatio-temporal dynamics inherent in the proposed models (Thomas *et al.*, 2010).

In southwest Tasmania, a comprehensive series of pollen and charcoal records have provided an excellent picture of the distribution of broad vegetation types throughout the Quaternary at regional scales (see Fletcher and Thomas, 2010a and references therein). However, these palaeoecological studies are limited in their ability to detect vegetation transitions on

localised vegetation boundaries. The only other historical ecology study in the region incorporating an explicit temporal scale is that of Brown *et al.* (2002), who investigated floristic and structural changes in vegetation in a spatially restricted set of monitoring plots over 20 years between 1980 and 2000. Whilst place-for-time chronosequences have provided some inferential information on the temporal relationships between fire, vegetation and soil (e.g. Brown and Podger, 1982a; Bowman *et al.*, 1986; Balmer, 1990; Brown *et al.*, 2002), these studies are a poor substitute for real data on vegetation change in the landscape (Johnson and Miyanishi, 2008).

Investigations into the feedbacks between fire frequency and vegetation central to the Jackson and Mount models are limited to characterisations of the flammability of some vegetation types (reviewed by Pyrke and Marsden-Smedley, 2005) and estimates of time-since-fire derived from tree ring counts (Gilbert, 1959; Jackson, 1968; Brown and Podger, 1982a; Jarman *et al.*, 1988; Brown *et al.*, 2002). Broad scale fire maps are available for the region (Marsden-Smedley, 1998) but these cannot be translated into vegetation specific fire frequencies in forested communities. Interactions between fire, vegetation and physical soil characteristics in southwest Tasmania have been studied at the landscape scale (di Folco, 2007) but studies of interactions with soil nutrients are limited to a suite of highly localised transects across vegetation boundaries (Bowman *et al.*, 1986; reviewed by Jackson, 2000). To date, there have been no formal attempts to test the relationships between fire, vegetation and physical environmental factors such as topography, drainage and geology at the landscape scale.

Study aims and thesis outline

The World Heritage landscapes of southwest Tasmania provide an ideal model system in which to study the effect of fire on shaping the distribution of coexisting fire-sensitive and fire-adapted vegetation communities. The influential model of vegetation dynamics that Jackson (1968) proposed for this region has been widely accepted in the literature, but the evidentiary basis for this widespread acceptance is lacking, particularly regarding the spatio-temporal resolution of field studies.

The aims of this thesis are to:

- (1) contribute new evidence on the decadal, century and millennial scale dynamics of southwest Tasmanian vegetation communities; and
- (2) investigate the role of interactions between fire, vegetation, soil and the physical environment in determining observed vegetation distributions and dynamics.

Importantly, this thesis does not aim to resolve the debate over the relative merits of the Jackson (1968) or Mount (1979) models. This is an impossible task in landscapes where key processes in the model operate over very long timescales. Instead, it uses the concepts and hypotheses put forward in these models as a framework for discussion of the vegetation dynamics of southwest Tasmania.

These aims of this thesis were carried out through four related projects conducted at a range of spatial scales (Figure 1.1) in southwest Tasmania. These are presented as four distinct chapters as follows:

Chapter 2 uses geospatial analysis of the spatial distribution of rainforest and the spatial pattern of a series of four very large fires to investigate the role of *fire-vegetation feedbacks* and *interactions between fire, vegetation and topography* in determining the distribution and maintenance of vegetation communities.

Chapter 3 uses repeat image analysis of aerial photographs and satellite imagery from 1948, 1988 and 2010 to quantify *decadal scale vegetation dynamics*. Geospatial analyses developed in Chapter 2 are used to explore the effect of *fire-vegetation-topography interactions* on observed dynamics. Analyses of soil samples collected across thirty-four boundaries included in the repeat image analysis are used to investigate the role of *fire-vegetation-soil feedbacks*.

Chapter 4 tests the applicability of using stable carbon isotopes in radiocarbon dated organic soil profiles for detecting *millennial scale transitions* between vegetation communities. This chapter also provides insights into the role of *fire-vegetation-soil feedbacks* using the physical and chemical characteristics of soil samples collected across two vegetation boundaries.

Chapter 5 investigates the special case of ‘mixed’ eucalypt-rainforest communities. Dendro-ecological techniques are used to characterise the age and pattern of stem growth of a stand of old-growth *Eucalyptus regnans* in southern Tasmania. The longevity of the eucalypt overstorey has implications for the *century scale dynamics* of these systems by dictating the rate of the transition from flammable eucalypt to fire-resistant rainforest vegetation.

Chapter 6 provides a synthesis of the key findings from these projects with other ecological studies in the region and discusses the implications for the proposed models of vegetation dynamics for southwest Tasmania and for the management of the Tasmanian Wilderness World Heritage Area.

The four core chapters of the thesis are written as papers, all of which are published in journals. For this reason, there is some repetition in the introduction and methods sections of the data chapters, as well as slight inconsistencies in format and style associated with specific journal requirements.

Chapter 2: Firescape ecology: how topography determines the contrasting distribution of fire and rainforest in the southwest of the Tasmanian Wilderness World Heritage Area

This chapter has been published as:

Wood, S.W., Murphy, B.M., and Bowman, D.M.J.S. (2011) Firescape ecology: how topography determines the contrasting distribution of fire and rainforest in the southwest of the Tasmanian Wilderness World Heritage Area. *Journal of Biogeography*. **38**, 1807-1820.

Abstract

Aim: To test the hypothesis that ‘islands’ of fire-sensitive rainforest are restricted to topographic fire refugia and investigate the role of topography–fire interactions in fire-mediated alternative stable state models.

Location: A vegetation mosaic of moorland, sclerophyll scrub, wet sclerophyll eucalypt forest and rainforest in the rugged, fire-prone landscapes of southwest Tasmania, Australia.

Methods: We used geospatial statistics to (1) identify the topographic determinants of rainforest distribution on nutrient-poor substrates, and (2) identify the vegetation and topographic variables that are important in controlling the spatial pattern of a series of very large fires (>40,000 ha) that were mapped using Landsat Thematic Mapper (TM) satellite imagery.

Results: Rainforest was more likely to be found in valleys and on steep south-facing slopes. Fires typically burned within highly flammable treeless moorlands and stopped on boundaries with less flammable surrounding vegetation types such as wet sclerophyll forest and rainforest. Controlling for the effect of vegetation, fires were most likely to burn on flats, ridges and steep north-facing slopes and least likely to burn in valleys and on steep south-facing slopes. These results suggest an antagonism between fire and rainforest, in which rainforest preferentially occupies parts of the landscape where fire is least likely to burn.

Main conclusions: The distribution of rainforest on nutrient-poor substrates was clearly related to parts of the landscape that are protected from fire (i.e. topographic fire refugia). The relative flammability of vegetation types at the landscape scale offers support to the proposed hierarchy of fire frequencies (moorland > scrub > wet sclerophyll > rainforest) that

underpin the ecological models proposed for the region. The interaction between fire occurrence and a range of topographic variables suggests that topography plays an important role in mediating the fire–vegetation feedbacks thought to maintain vegetation mosaics in southwest Tasmania. We suggest that these fire–topography interactions should be included in models of fire-mediated alternative stable vegetation states in other fire-prone landscapes.

Introduction

Fire is an integral factor influencing global ecosystem patterns and processes (Bowman *et al.*, 2009) and a significant proportion of the world’s vegetation owes its distributional patterns and structural attributes to specific fire regimes (Bond and Keeley, 2005; Bond *et al.*, 2005). At landscape scales, interactions between fire and vegetation often result in vegetation mosaics of fire-adapted vegetation communities, interspersed with fire-sensitive vegetation communities (Bowman, 2000). In fire-prone landscapes, which we call ‘firescapes’, the topographic characteristics of the landscape (e.g. slope, aspect, topographic position) play an important role in determining the distribution of vegetation and biodiversity (Coblentz and Riitters, 2004) because of their role as one of the key factors controlling the spread of fire (Cary *et al.*, 2006) and the spatial distribution of topographic fire refugia (Bowman, 2000).

Fire is particularly pervasive in shaping vegetation patterns in Australia (Bradstock *et al.*, 2002) and has been implicated as the most critical factor controlling the fragmentary distribution of fire-sensitive rainforest within vast tracts of flammable sclerophyll vegetation from the monsoonal north to the temperate south (Bowman, 2000). Central to the development of this hypothesis are observations of rainforests being restricted to parts of the landscape that offer topographic fire protection (i.e. fire refugia). In Australia, researchers have consistently reported links between ‘islands’ of rainforest and particular topographic

attributes (e.g. steep valleys, particular aspects, rocky outcrops) based on correlations between rainforest occurrence and various metrics that describe topographic variation (Webb, 1968; Ash, 1988; Russell-Smith, 1991; Fensham, 1995; Bowman, 2000; Lindenmayer *et al.*, 2000a; Clarke, 2002; Brook and Bowman, 2006). Similar findings have been reported for spatially restricted pockets of fire-sensitive species in other fire-prone landscapes throughout the world (e.g. Geldenhuys, 1994; Perry and Enright, 2002; Coblenz and Keating, 2008). However, whilst these studies conclude that specific topographic configurations provide fire refugia, these conclusions are largely inferential given that they rely on a priori assumptions regarding the effect of topography on fire spread, rather than explicitly incorporating quantitative evidence on what actually constitutes topographic fire protection in the particular landscape in question.

Remote sensing can be used to measure and relate the spatial pattern of fire to key drivers across landscapes (Verbyla *et al.*, 2008; Bradstock *et al.*, 2010). For example, the mapping of fire scars from high resolution satellite imagery such as Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper (ETM+) has been used to evaluate the effect of localized topographic features (i.e. slope, aspect, elevation) and vegetation characteristics on the spread and severity of wildfires in a range of landscapes (e.g. Díaz-Delgado *et al.*, 2004; Collins *et al.*, 2007; Maingi and Henry, 2007; Viedma, 2008; Bradstock *et al.*, 2010). Other studies have used broad-scale topographic indices, such as topographic roughness (see Guyette *et al.*, 2002), to investigate how the degree of topographic variability affects fire occurrence and burnt area at regional or continental scales (Dickson *et al.*, 2006; Russell-Smith *et al.*, 2007; Archibald *et al.*, 2009). Thus, the analysis of satellite-mapped fire scars can be used to characterize the topographic attributes of the landscape terrain that have a low likelihood of carrying fire, i.e. fire refugia. In this study we develop an analytical framework for incorporating information on the relationship between topographic features and fire data

derived from satellite-mapped fire scars to test the hypothesis that the distribution of fire-sensitive rainforest is related to topographic fire refugia in an archetypical ‘firescape’ in the southwest of Australia’s largest island, Tasmania.

Southwest Tasmania is a mountainous and perennially wet region of high conservation value that forms a large part of the Tasmanian Wilderness World Heritage Area (Brown, 1996). This region has an ideal climate for temperate rainforest, and it has been argued that even on nutrient-poor substrates, there is no aspect, soil-type or edaphic situation that could not support rainforest (Jackson, 1968). However, a large proportion of the lowlands of this region consist of flammable treeless sedge/heath ‘moorlands’, sclerophyll scrub and eucalypt forests, with fire-sensitive *Nothofagus*-dominated rainforests limited to fragmented pockets across the landscape (Figure 2.1). The decoupling of vegetation from the prevailing climate is inextricably linked to a long history of landscape fire (Jackson, 1968; Fletcher and Thomas, 2010a). Ecologists working in this region have long used observations of rainforest being confined to steep valleys and protected slopes to invoke the concept of topographic fire refugia (Casson, 1952; Gilbert, 1959; Jackson, 1968; Mount, 1979; Brown and Podger, 1982a; Read, 1999; Brown *et al.*, 2002). However, a rigorous quantitative analysis to test the efficacy of these qualitative observations has yet to be undertaken. Understanding the relationship between fire, topography and rainforest distribution is of critical importance to inform the management of this World Heritage Area (Brown, 1996), particularly in relation to evaluating the vulnerability of fire-sensitive vegetation types to unplanned wildfire and prescription burning practices (King *et al.*, 2006).

The vegetation mosaic of southwest Tasmania has been put forward by Jackson (1968) as an exemplar of an ecosystem in which alternative stable vegetation states are maintained by positive feedbacks between vegetation and fire disturbance (see also Bowman and Jackson,

1981; Bowman and Wood, 2009). Alternative stable vegetation states that are maintained by fire have been proposed for a range of terrestrial ecosystems from around the world (Wilson and Agnew, 1992; Petraitis and Latham, 1999; Perry and Enright, 2002; Beckage and Ellingwood, 2008; Warman and Moles, 2009; Odion *et al.*, 2010), but the ecological model proposed by Jackson (1968) is one of the earliest attempts (see also Mutch, 1970) to formally explain the long-term resilience and potentially rapid transitions predicted by alternative stable state models in natural systems (Scheffer *et al.*, 2001; Beisner *et al.*, 2003). In brief, Jackson's (1968) model recognises six vegetation types in southwest Tasmania, summarised here to four dominant communities: sedge/heath moorlands, sclerophyll scrub, wet sclerophyll eucalypt forest and rainforest. Each vegetation community actively modifies the rate of fuel accumulation and fuel characteristics (i.e. fire frequency), soil nutrient capital and light environment in a direction that enhances its own growth and survival, and simultaneously hinders or constrains other vegetation types (Figure 1.4c). Jackson (1968) suggested that these positive feedbacks collectively encourage an inherent resilience to change in southwest Tasmanian vegetation communities, but also included the possibility that chance deviations in fire frequencies – assumed to be highly improbable – can push an otherwise stable vegetation community beyond its 'resilience threshold' and cause a shift to another vegetation community (see Figure 1.4c).

Implicit within fire-driven alternate stable states models is the role of environmental parameters such as rainfall, seasonality, soil type and topography in mediating positive feedback processes (Warman and Moles, 2009). In topographically complex landscapes, terrain characteristics are particularly important in influencing vegetation–fire interactions through their fundamental control on fire behaviour. Jackson (1968) incorporated this dynamic into his model by assuming that fire frequency and thus the occurrence of each vegetation type will reflect the topographic pattern across the landscape. Accordingly,

rainforest would be restricted to fire protected slopes and valleys, and at the other extreme, moorlands would be more likely to occur on ridge tops and north-facing slopes that are exposed to fire carrying winds and the drying effects of increased solar radiation. In effect, these interactions may comprise an added degree of resilience within the various vegetation communities. Whilst Jackson (1968) allowed for vegetation transitions despite these topographic controls, an alternative ‘stable fire cycles’ model put forward by Mount (1979) posited that the effects of topography and other physical environmental variables (i.e. geology and hydrology) on fire frequency were strong enough to eliminate the chance transitions to alternative vegetation communities resulting in long-term stability in vegetation patterns (see Figure 1.4c).

The objective of this paper is to use southwest Tasmania as a model ‘firescape’ to understand the relationships between fire, topography and vegetation, with particular emphasis on their effect on the distribution of fire-sensitive rainforest vegetation. Specifically, we use geospatial statistics to (1) identify the topographic determinants of rainforest distribution over a large area (~ 540,000 ha) on the nutrient-poor geologies of southwest Tasmania, and (2) identify the vegetation and topography variables that are important in controlling the spatial pattern of a series of very large fires (> 40,000 ha) in southwest Tasmania that were mapped using Landsat TM satellite imagery. Our findings will be used to investigate (i) the role of topographic fire refugia as an underlying mechanism determining rainforest distribution, (ii) how the pattern of fire in the landscape is influenced by topography and the different flammabilities of dominant vegetation communities, and (iii) how these interactions contribute to our understanding of ecological models proposed for the region (Jackson, 1968; Mount, 1979) and models of alternative stable vegetation states in other fire-prone ecosystems.

Methods

Study area

The southwest Tasmanian study area is located within the Tasmanian Wilderness World Heritage Area (Figure 2.1). Southwest Tasmania is topographically complex and the region is dominated by large areas of highly metamorphosed, nutrient-poor Precambrian basement rocks (Pemberton, 1989). The soils of the region are dominated by extensive areas of infertile organic soils that form shallow to deep surface horizons under all vegetation types (Pemberton, 1989). Southwest Tasmania has a cool maritime climate with winter and summer minimum and maximum temperatures of 3 °C and 10 °C, and 10 °C and 20 °C, respectively. Precipitation exhibits a winter peak, a strong east–west gradient, and an annual average of between 1500 and 3000 mm (King *et al.*, 2008). The vegetation mosaic consists of extensive tracts of highly flammable treeless moorlands (~35%) characterized by the sedge *Gymnoschoenus sphaerocephalus* and a diverse low heath vegetation; moderately flammable low sclerophyll scrub (~15%) and tall wet sclerophyll forests (~22%) characterized by *Eucalyptus nitida*, *Leptospermum nitidum*, *Leptospermum scoparium*, *Banksia marginata*, *Melaleuca squarrosa*; and fire-sensitive temperate rainforest (~23%) dominated by *Nothofagus cunninghamii* with other species including *Eucryphia lucida*, *Atherosperma moschatum* and *Phyllocladus aspleniifolius*. Coastal communities (~1%) and alpine and subalpine treeless vegetation (~ 1%) also occur throughout the study area.

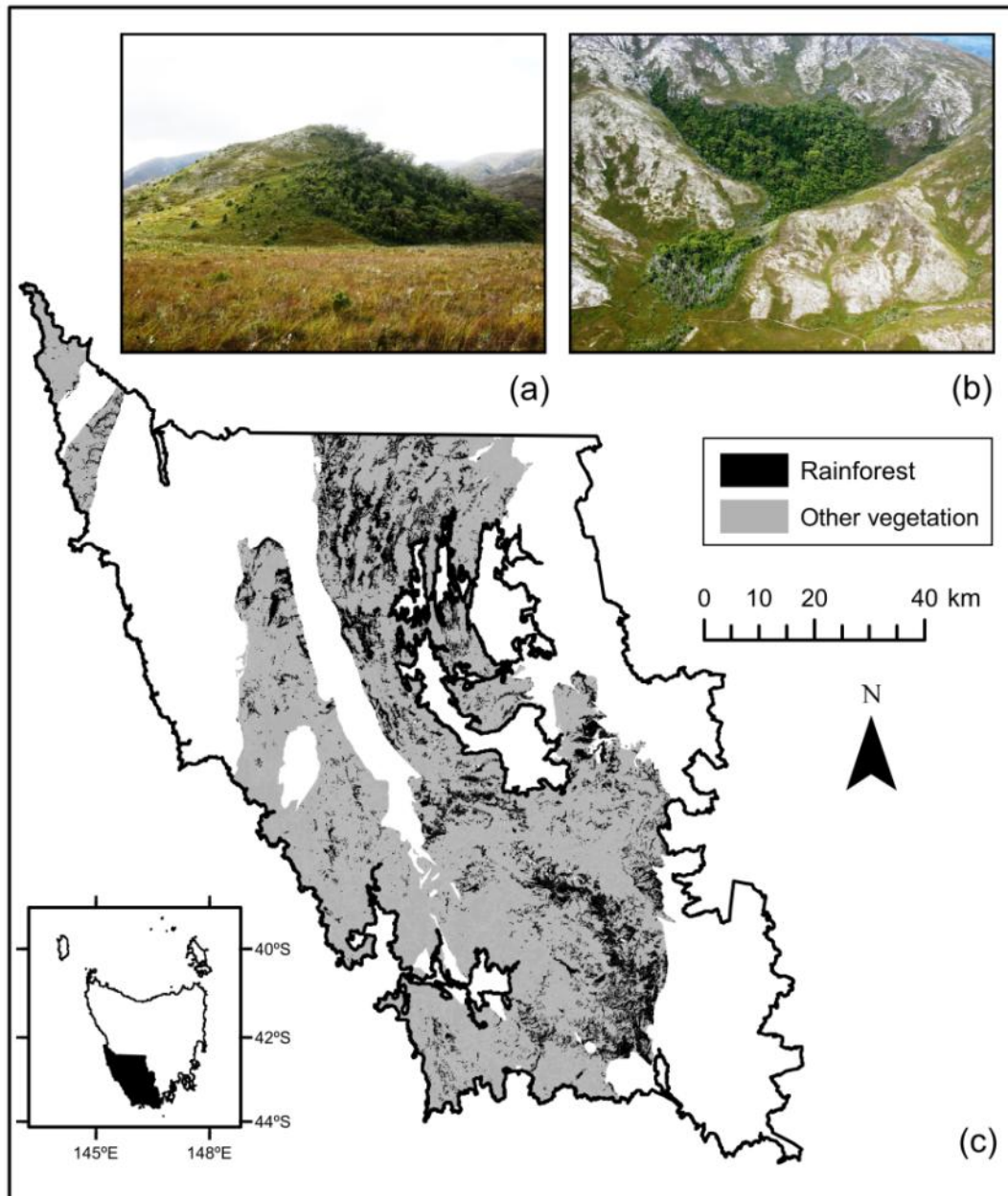


Figure 2.1. Photographs showing rainforest and wet sclerophyll vegetation restricted to (a) south-facing slopes and (b) steep-sided valleys in southwest Tasmania. The map (c) shows the location of the study area in southwest Tasmania (inset) and the distribution of rainforest (black) and other vegetation (grey) on Precambrian metamorphic geology and associated alluvial landforms. The study area is bounded by the Tasmanian Wilderness World Heritage Area and excludes Lake Pedder and Lake Gordon. The vegetation map was derived from the TASVEG mapping product (Harris and Kitchener, 2005).

General approach

We explored the relationships between rainforest occurrence and three topographic variables (topographic position, aspect, elevation) by applying the modelling approach for analysing spatially autocorrelated non-normal data developed by Murphy *et al.* (2010). This approach uses generalized autoregressive error models incorporated into the information-theoretic model selection framework (i.e. based on Akaike's information criterion, AIC, see Burnham and Anderson, 2002). Using the same modelling approach, we then examined the relationship between the spatial pattern of four large fires (~ 40,000 ha) and topography (topographic position, aspect, elevation), in an analytical framework that was *independent of vegetation type*. This independence was critical, because examination of the effect of topography on the spatial pattern of fire is implicitly confounded by differences in the flammability of different vegetation types. For example, a steep-sided valley may not burn because it is occupied by relatively non-flammable rainforest vegetation rather than because of the geometric shape of the landscape. To overcome this problem we followed the logic of Murphy *et al.* (2010) and focused on the relationships between the spatial pattern of fire and topography separately for each of the four dominant vegetation types in the landscape. This effectively decoupled fire and vegetation within the analytical framework and ensured that the relationships tested were restricted to the effects of topography on the spatial pattern of fire.

We hypothesized that, if the distribution of rainforest is related to topographic fire protection, then the separate analyses of rainforest distribution and the spatial pattern of fire should identify the same topographic correlates, but the directions of the relationships should be opposite. For example, fuel moisture is known to be higher on southern slopes in the Southern Hemisphere hence limiting fire spread (i.e. a negative relationship between fire occurrence and southerly aspect), and as a result, fire-sensitive rainforest is often associated

with southern slopes (i.e. a positive relationship between rainforest occurrence and southerly aspect).

Vegetation, geology and derived topographic attributes

Vegetation data for the study area were derived from the Tasmanian vegetation mapping product TASVEG, which was mapped primarily from 1:25,000 aerial photographs (Harris and Kitchener, 2005). Vegetation information was aggregated into four broad community groups: (1) moorland and sedgeland, (2) sclerophyll scrub and heathland, (3) wet sclerophyll eucalypt forest and woodland, and (4) rainforest. Other minor vegetation groups, including non-eucalypt forest and woodland, dry eucalypt forest and woodland, highland treeless vegetation and native grassland, covered only a small proportion of the landscape and were excluded from our analysis. Geology type was available for the study area at a coarse scale of 1:250,000. Rainforest occurs over a broad range of geologies and soils in southwest Tasmania, with large tracts existing on relatively fertile limestone and basalt and increasingly fragmentary distributions on shallow, infertile soils over Precambrian metamorphic rocks (Read, 2001). To avoid the possible confounding effects of geology on our rainforest distribution analysis, and given the emphasis that Jackson (1968) placed on nutrient-poor substrates, we restricted our study area to Precambrian metamorphic geologies and associated alluvial landforms (~540,000 ha; Figure 2.1). A 25-m resolution digital elevation model (DEM) was used to calculate three topographic variables: (1) topographic position, (2) a northness index, which combines aspect and slope, and (3) elevation (Table 2.1).

Variable	Data source
Topographic Position:	Topographic Position (Jenness, 2006) determined for each cell of a 25m DEM by calculating the difference between the elevation of the cell and the mean elevation calculated from all cells in a circular window of radius 200m centred on the cell of interest. Strongly positive TPI values are ridges. Strongly negative TPI values are valleys. TPI values around 0 were classified into flat, gentle, moderate and steep using the calculated slope of each cell derived from the 25m DEM.
A. Valley	
B. Ridge	
C. Flat (<5°)	
D. Gentle slope (5° to 15°)	
E. Moderate slope (15° to 30°)	
F. Steep slope (>30°)	
Northness Index	Northness Index (Holden <i>et al.</i> , 2009) was calculated as $slope \times \cos(aspect)$. Aspect (degrees) and slope (%) were calculated from 25m DEM. Steep North ~ 1, Steep South ~ -1, East and West and Flat ~ 0.
Elevation (m)	25m DEM.

Table 2.1. Topographic variables that were considered plausible correlates of rainforest distribution and the burnt area of four large fires in southwest Tasmania.

Fire	Date of fire	Image acquisition date		Landsat burnt area (ha)	Vegetation communities in burnt area (%)				
		Pre-fire	Post-fire		Moor	Scrub	Wet scl.	Rainforest	Other
Castor	Jan, 2006	Jun 22, 2005	May 24, 2006	2,699	56.7	16.4	20.4	2.3	4.2
Birches	Feb, 2007	Apr 16, 2004	Mar 08, 2007	2,335	93.6	0.9	1.2	0.8	3.5
Reynolds	Feb, 2007	Apr 16, 2004	Mar 08, 2007	23,226	64.8	9.8	14.8	9.6	1.0
Arthur	Feb, 2007	Apr 16, 2004	Mar 08, 2007	12,494	77.9	13.1	6.8	0.9	1.3
All Fires				40,754	69.9	10.7	11.9	5.9	1.6

Table 2.2. Details of four large fires that burned within the southwest Tasmania study area in 2006–07 and the acquisition dates for Landsat Thematic Mapper (TM) imagery used for mapping the fire scars. Burnt area was calculated from fire scars mapped from Landsat TM imagery (see Figure 2.2). All images were from Landsat TM Path 91/Row 90. Dominant vegetation communities were classified according to the TASVEG mapping product (Harris and Kitchener, 2005; see Figure 2.3). Wet Scl represents Wet Sclerophyll.

Mapping of fire scars

We used Landsat TM satellite imagery to map the extent of four large fires that occurred within the southwest Tasmania study area between January 2006 and February 2007 (Table 2.2). Large wildfires such as these are relatively uncommon in this region, with about a dozen large fires recorded between 1940 and 2000 (Marsden-Smedley, 1998; Marsden-Smedley and Kirkpatrick, 2000). The fires we analysed burnt under weather conditions that are considered typical of those conducive to large fires in this region, that is, they were ignited by lightning strikes during the summer–autumn season and were largely driven by hot and dry north to north-westerly winds. Given the absence of even the most rudimentary roads in the region, these fires were allowed to burn freely without fire suppression, with the exception of a few small accessible sections on the north-eastern flank of the Arthur fire. Thus we were afforded a rare opportunity to examine the influence of vegetation and topography on the spatial pattern of fire under relatively natural conditions.

The pre-fire and post-fire satellite data used in this study were obtained from the Landsat TM satellite series available at United States Geological Survey Earth Resources Observation and Science Centre (USGS EROS: <http://eros.usgs.gov/>; March 2010). Image acquisition was limited by the prevalence of cloud obscuring large parts of this perennially wet region. We attempted to find combinations of pre-fire and post-fire images (Table 2.2) that: (1) were close to anniversary dates (i.e. April 2006–April 2007); (2) had post-fire images close to the fire date; and (3) were separated by as few years as possible (e.g. Rogan *et al.*, 2002; Epting *et al.*, 2005). Landsat images were processed by USGS EROS Data Centre to Level 1 Terrain (LIT), meaning that the data had been radiometrically corrected (to top of atmosphere reflectance values), geometrically corrected, and orthorectified.

The extent of each fire was estimated using the differenced normalized burn ratio (dNBR), which is an index based on the normalized burn ratio (NBR). These indices are commonly used to map burnt and unburnt areas from remotely sensed imagery (e.g. Key and Benson, 2006; Collins *et al.*, 2007; French *et al.*, 2008; Hoy *et al.*, 2008; Verbyla *et al.*, 2008). The NBR index responds to the substantial decrease in near-infrared reflectance (NIR: Landsat TM Band 4) and a substantial increase in shortwave infrared reflectance (SWIR: Landsat TM Band 7) due to plant canopy damage by fire, and was calculated as $NBR = (NIR - SWIR) / (NIR + SWIR)$. The dNBR index effectively normalizes for variations in pre-fire vegetation cover, which is important in landscapes with treeless areas such as the moorlands in southwest Tasmania, and was calculated as $dNBR = (NBR \text{ pre-fire} - NBR \text{ post-fire})$.

We generated histograms of the frequency distribution of dNBR in the vicinity of each of the four fires (Figure 2.2, inset). These histograms exhibited a bimodal distribution, which clearly discriminated unburnt pixels (low dNBR peak) from burnt pixels (high dNBR peak). Each image was reclassified as burnt and unburnt using these histograms to produce maps of the extent of each fire scar (Figure 2.2). Given the size and remote location of these fires, detailed field validation of the mapped fire area was considered impractical. Instead, we validated three out of the four fire scar perimeters with post-fire GPS helicopter surveys conducted by the Tasmanian Fire Branch of the Parks and Wildlife Service (A. Pyrke, Tasmanian Parks and Wildlife Service, pers. comm.).

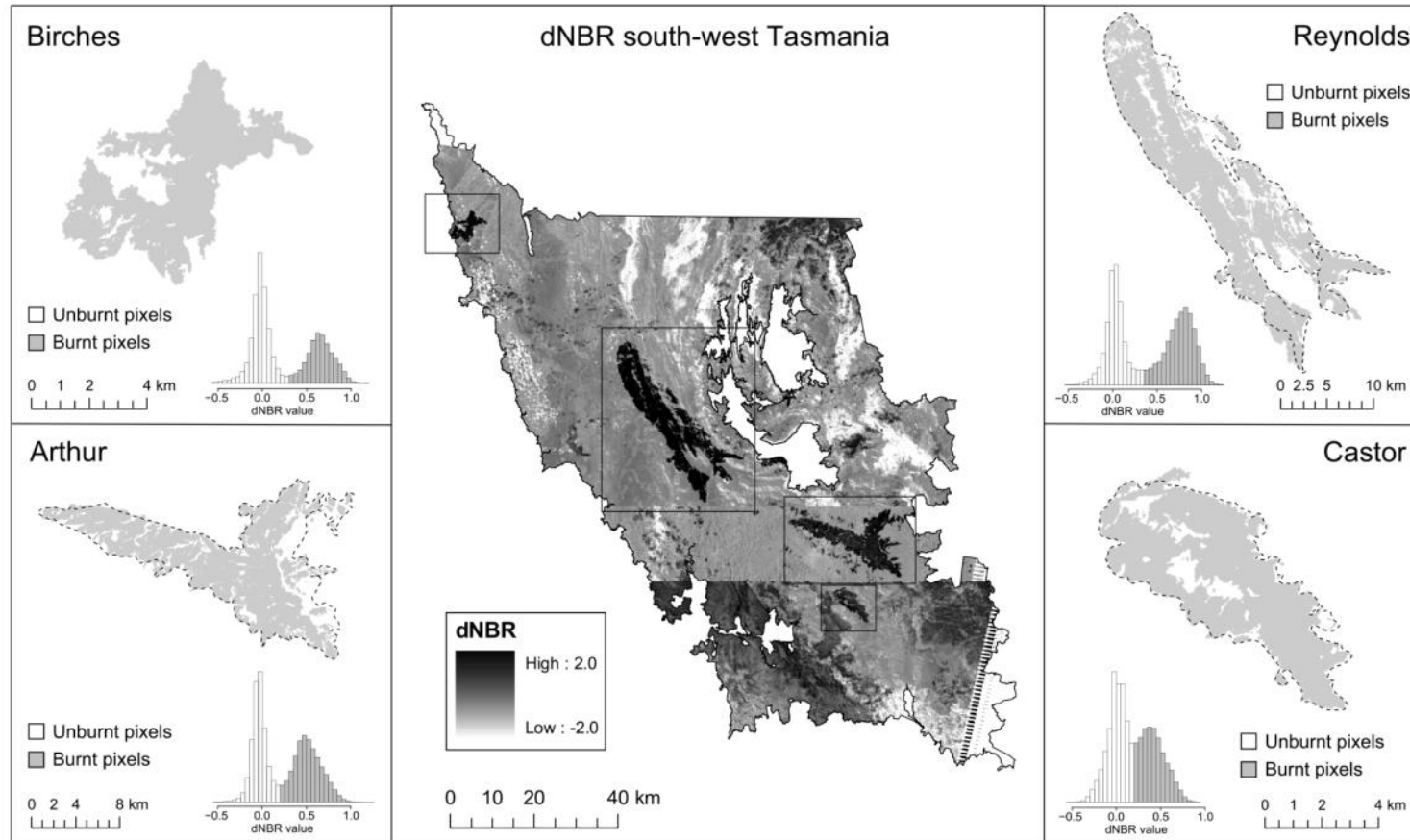


Figure 2.2. The differenced normalized burn ratio (dNBR) surface calculated from Landsat Thematic Mapper (TM) imagery for southwest Tasmania (centre panel), where high dNBR values (i.e. black shading) are burnt areas. Bimodal histograms of dNBR pixel values in the vicinity of each fire (inset) were used to classify the image into burnt (grey bars) and unburnt (white bars) areas. The four fire scar footprints are shown (outer panels) along with the helicopter GPS mapped perimeter of three of the four fires provided by Tasmanian Parks and Wildlife Service (dashed line). The dNBR map is a mosaic of three satellite images, hence the vertical discontinuity in the dNBR surface.

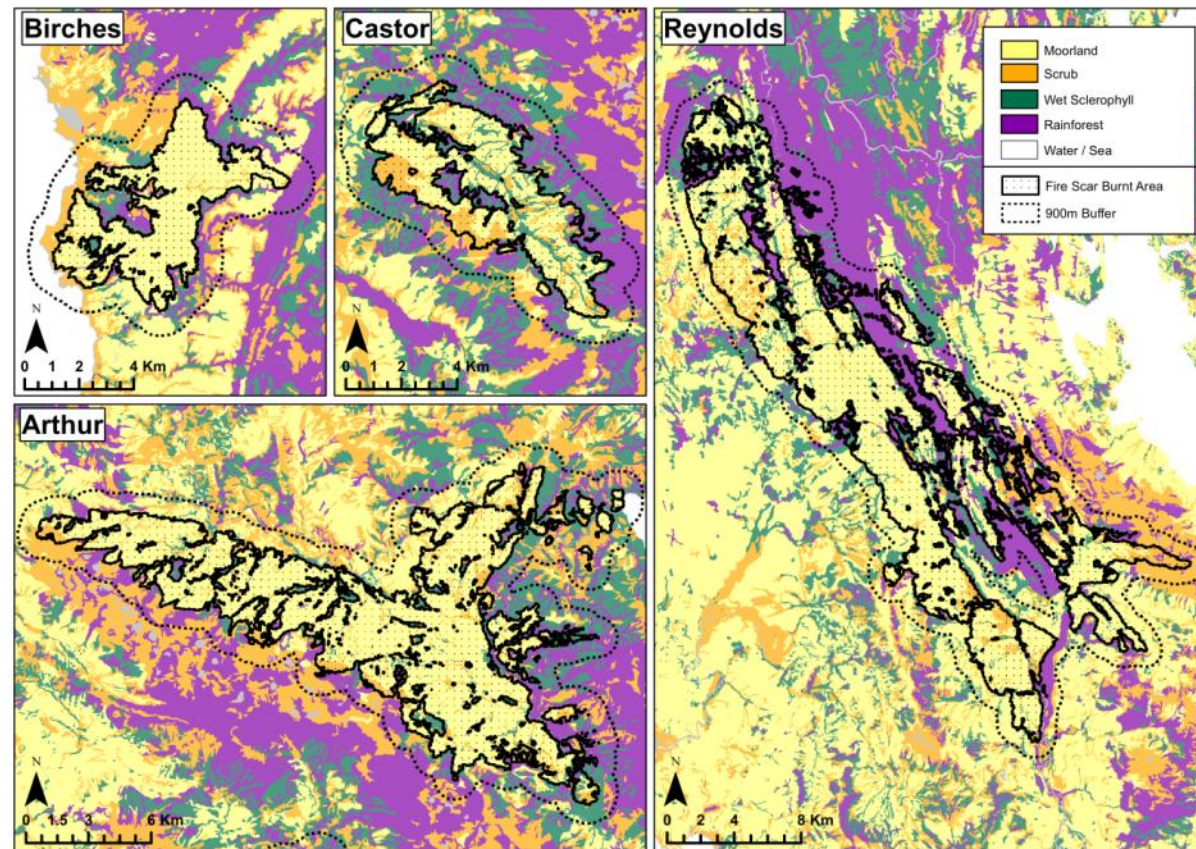


Figure 2.3. Detailed map of four fire scars in southwest Tasmania showing the extent of the fire scars (dotted with black perimeter) and the 900 m buffer used in the fire scar analysis (dashed black line). The four vegetation communities used in the analysis are shown. The vegetation map was derived from the TASVEG mapping product (Harris and Kitchener, 2005). For illustration purposes, alpine communities and coastal communities were included in the ‘scrub’ classification in these maps. These particular communities made up ~1% of the landscape and were not included in any analyses.

Sampling design and statistical analysis

Our approach was to compare two analyses – one focusing on the distribution of rainforest and the other focusing on the spatial patterns of fire scars – to investigate the effect of interactions between fire and topography on controlling rainforest distribution in southwest Tasmania. For the rainforest distribution analysis, 4000 sampling points were randomly allocated to the area of Precambrian metamorphic geology in southwest Tasmania and each point was attributed with a presence/absence of rainforest vegetation (Figure 2.1) and the topographic attributes derived from the DEM (Table 2.1). These attributed points were used to examine the effect of topographic variables on the distribution of rainforest in the modelling analysis outlined below.

Our fire scar analysis was based on (1) the combined burnt area of all four fire scars (~40,000 ha); and (2) an equivalent area (~40,000 ha) of unburnt vegetation contained within a buffer zone 900-m wide around the mapped perimeter of the four fire scars (Figure 2.3). The 900-m buffer included unburnt vegetation ‘islands’ within the main fire scar. To examine the effect of vegetation (moorland, scrub, wet sclerophyll and rainforest) on the spread of fire we randomly allocated 10,000 points to the combined area of the fire scar and buffer, and calculated the proportion of the points in each vegetation community for (1) the burnt area of the fire scar and (2) the area contained within unburnt 900 m buffer. To examine the effect of topography on fire *independent of vegetation type*, we randomly allocated an independent set of 4000 points to the total area of each vegetation community (moorland, scrub, wet sclerophyll and rainforest) within the combined area of the fire scar and buffer. Each point was attributed with the presence/absence of fire and the topographic variables (Table 2.1) and submitted to the modelling analysis outlined below.

Modelling of rainforest and fire

Models representing all combinations, without interactions, of the three variables considered important correlates of rainforest distribution and fire occurrence, respectively, (i.e. topographic position, aspect, elevation) were constructed as generalized autoregressive error (GAR_{err}) models. This type of model has recently been developed by Murphy *et al.* (2010) to analyse spatially autocorrelated non-normal data. It is analogous to the simultaneous autoregressive error model for normal data (Cressie, 1993), but can cope with non-normal data types in the same way as a generalized linear model. Both rainforest and fire occurrence represented presence/absence data, and were modelled using binomial errors. We evaluated the extent to which the GAR_{err} models successfully accounted for residual spatial autocorrelation using correlograms based on Moran's *I* (Dormann *et al.*, 2007; Appendix 2).

Models were evaluated using AIC_c, a robust second order form of AIC, a model selection index favouring both model fit and model simplicity (Burnham and Anderson, 2002). Lower values of AIC_c indicate greater support for a model, relative to other models in the same candidate set. From AIC_c, Akaike weights (w_i) were calculated for each model, and these are equivalent to the probability of a given model being the best in the candidate set. The importance of each variable was evaluated by calculating w_+ , the sum of w_i for all models in which that variable occurred. For each variable, w_+ is equivalent to the probability of the best model containing that variable, and is a useful expression of the weight of evidence for the importance of the variable. We considered that w_+ values of < 0.73 were indicative of substantial model selection uncertainty, and that a relationship between the response and the explanatory variable in question was not well supported by the data. A w_+ value of 0.73 is equivalent to an AIC_c difference of two units between the models containing the variable

under examination and those not containing it. An AIC_c difference of two units is a common ‘rule of thumb’ used by ecologists to assess clear evidence of an effect (Richards, 2005).

Results

Correlates of rainforest distribution

Rainforest occurrence was clearly correlated with several topographic variables. Model selection favoured the model containing the variables topographic position ($w_+ = 1.00$) and the northness index ($w_+ = 1.00$) and this model explained 11% of the null model deviance (Table 2.3). There was little evidence of a relationship between rainforest occurrence and elevation ($w_+ = 0.34$). According to the selected model, rainforest was most likely to occur in valleys, followed by steep and moderate slopes and least likely to occur on gentle slopes, ridges and flats (Figure 2.4a). The relationship between the northness index and rainforest was strongly negative, indicating that rainforest is much more likely to be found on steep southern slopes compared to steep northern slopes (Figure 2.4b).

Fire and vegetation

The mapped area of the four fires (Figure 2.2 and 2.3) covered 40,754 hectares, with moorland vegetation making up a large proportion of the total burnt area of each fire (Table 2.2). There was a high level of congruence between satellite-mapped fire scars and the fire perimeter obtained by the helicopter GPS survey (Figure 2.2). The vast majority of the 10,000 points that were within the burnt area were classified as moorland (70%), with rainforest making up just 8% of points (Figure 2.5a). Conversely, only 20% of points in the unburned buffer were moorland (Figure 2.5b), with a higher proportion of points classified as wet sclerophyll (21%) or rainforest (33%). The ratio of the burnt and unburnt points on each

Topographic	Rainforest	Fire occurrence (w_+)			
variable	(w_+)	Moorland	Scrub	Wet Scl.	Rainforest
Topographic position	1.00	1.00	1.00	1.00	1.00
Northness index	1.00	0.98	0.90	1.00	1.00
Elevation	0.34	1.00	1.00	1.00	1.00

Table 2.3. Importance values (Akaike weights, w_+) for topographic variables to explain rainforest distribution and fire occurrence in the four dominant vegetation types. All variables with a reasonable level of support as predictors of the response variable ($w_+ \geq 0.73$) are shown in bold. Wet Scl represents Wet Sclerophyll.

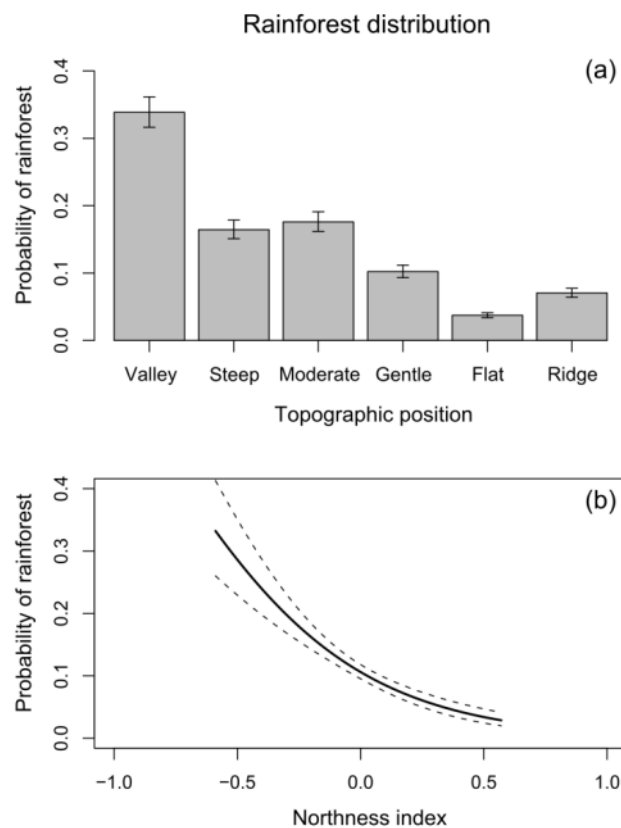


Figure 2.4. The modelled relationship between the predicted probability of rainforest and (a) topographic position and (b) northness index. The northness index represents a gradient from steep southern slopes (strongly negative values) to steep northern slopes (strongly positive values). 95% confidence intervals are shown.

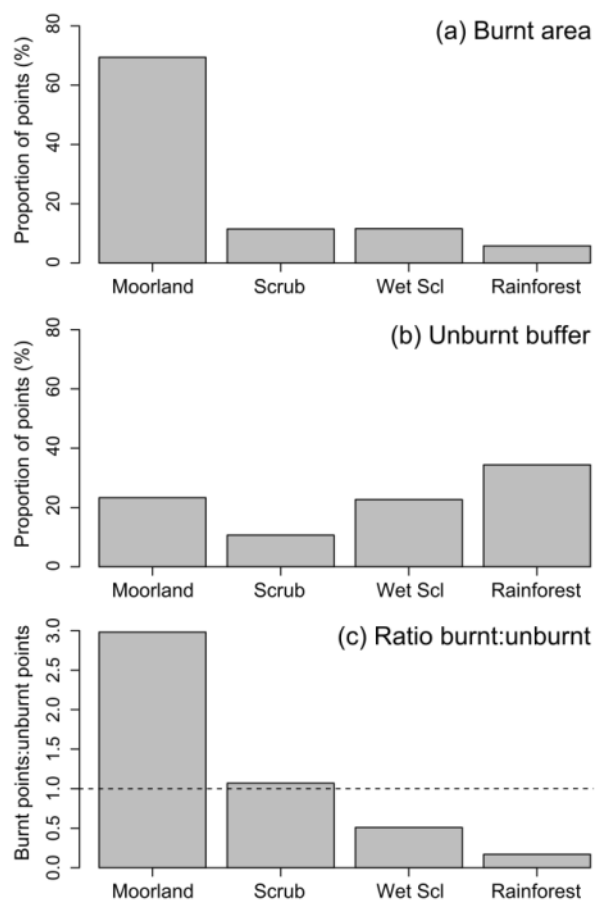


Figure 2.5. Proportion of points within each vegetation community in (a) the burnt area of the fire scar ($n = 4762$) and (b) the unburnt 900-m buffer around the perimeter of the fire scar ($n = 4880$; see Figure 2.3). The ratio of burnt and unburnt points ($n = 9542$) for each vegetation type is illustrated in panel (c). A ratio of 1 represents an equal proportion of points that are burnt and unburnt (i.e. moderately flammable). A ratio > 1 represents proportionally more burnt points than unburnt points (i.e. highly flammable). A ratio < 1 represents proportionally less burnt points than unburnt points (i.e. low flammability). Wet scl, wet sclerophyll.

side of the fire scar perimeter (Figure 2.5c) is an index of flammability for each vegetation class and it decreased from moorland (> 1) to scrub (~ 1) to wet sclerophyll (< 1) and rainforest ($<< 1$). The proportion of points in each vegetation community that were classified as burnt was 75% (moorland), 52% (scrub), 34% (wet sclerophyll) and 14% (rainforest).

Correlates of burnt area

For each vegetation type, model selection favoured the global model containing the variables topographic position, the northness index and elevation ($w_+ > 0.90$ in all cases; Table 2.3). The selected models for fire occurrence in moorland, scrub, wet sclerophyll and rainforest explained 11%, 5%, 12% and 6% of the null model deviance, respectively. Predictions from the selected models developed independently within each vegetation type indicated generally consistent trends, with fires least likely to burn in valleys, and most likely to burn on flats and/or ridges (Figure 2.6a). The models showed that fire was more likely to burn on steep northern slopes compared to steep southern slopes (Figure 2.6b) and the probability of fire decreased with increasing elevation for all vegetation types except moorland (Figure 2.6c).

Relationship between modelled probability of rainforest and fire

Our analyses indicated that topographic position and the northness index were important correlates of both rainforest distribution and the spatial pattern of fire, and that the direction of the modelled relationships were generally opposite (compare Figures 2.4 and 2.6). As such, there was a clear negative relationship between the predicted probability of rainforest and the predicted probability of fire for all vegetation types in the landscape (Figure 2.7).

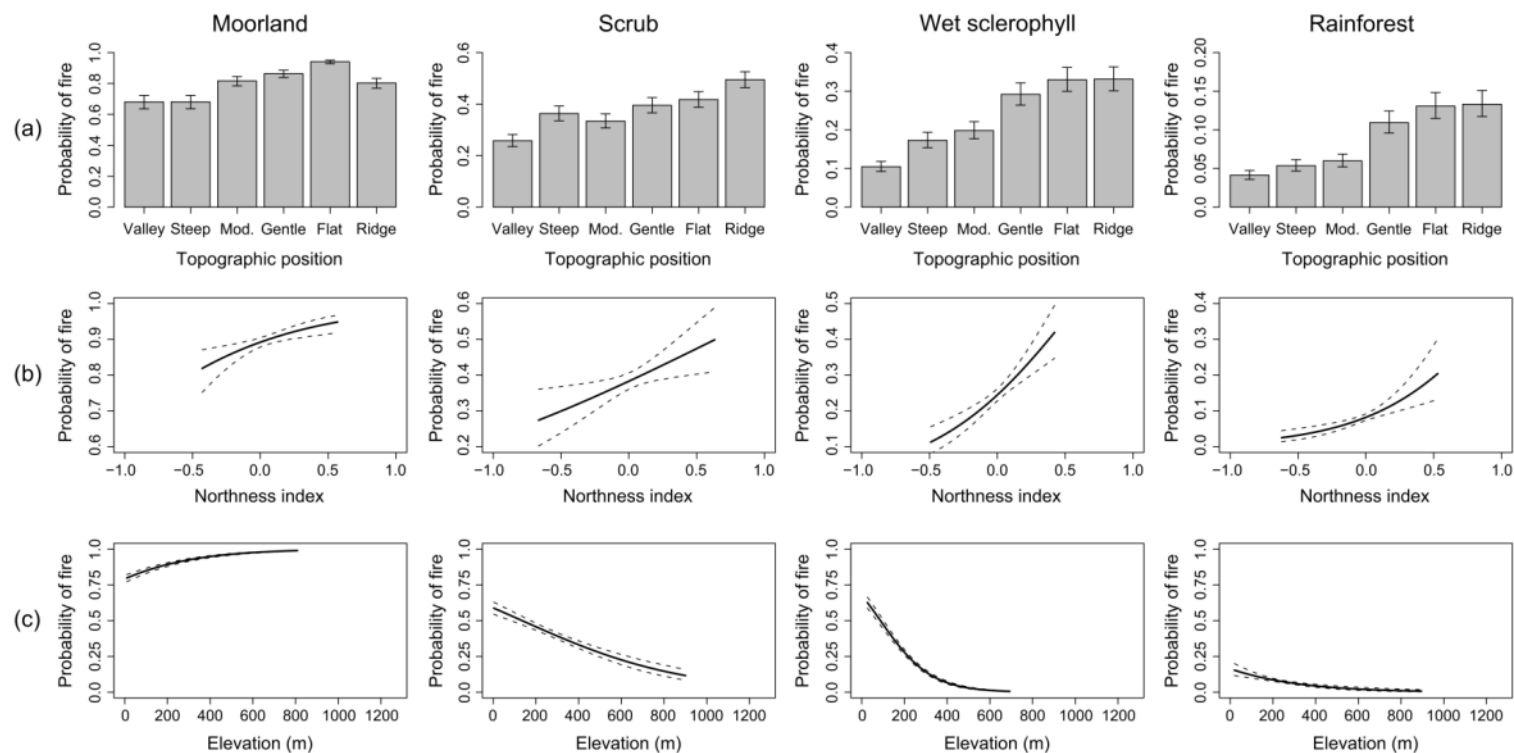


Figure 2.6. The modelled relationship between fire occurrence and (a) topographic position, (b) northness index and (c) elevation, for the selected models for the four dominant vegetation communities in southwest Tasmania. The northness index represents a gradient from steep southern slopes (strongly negative values) to steep northern slopes (strongly positive values). 95% confidence intervals are shown. Note the difference in y-axis scales across vegetation types, which is a reflection of their relative flammability. The topographic position ‘Mod.’ refers to moderate slopes.

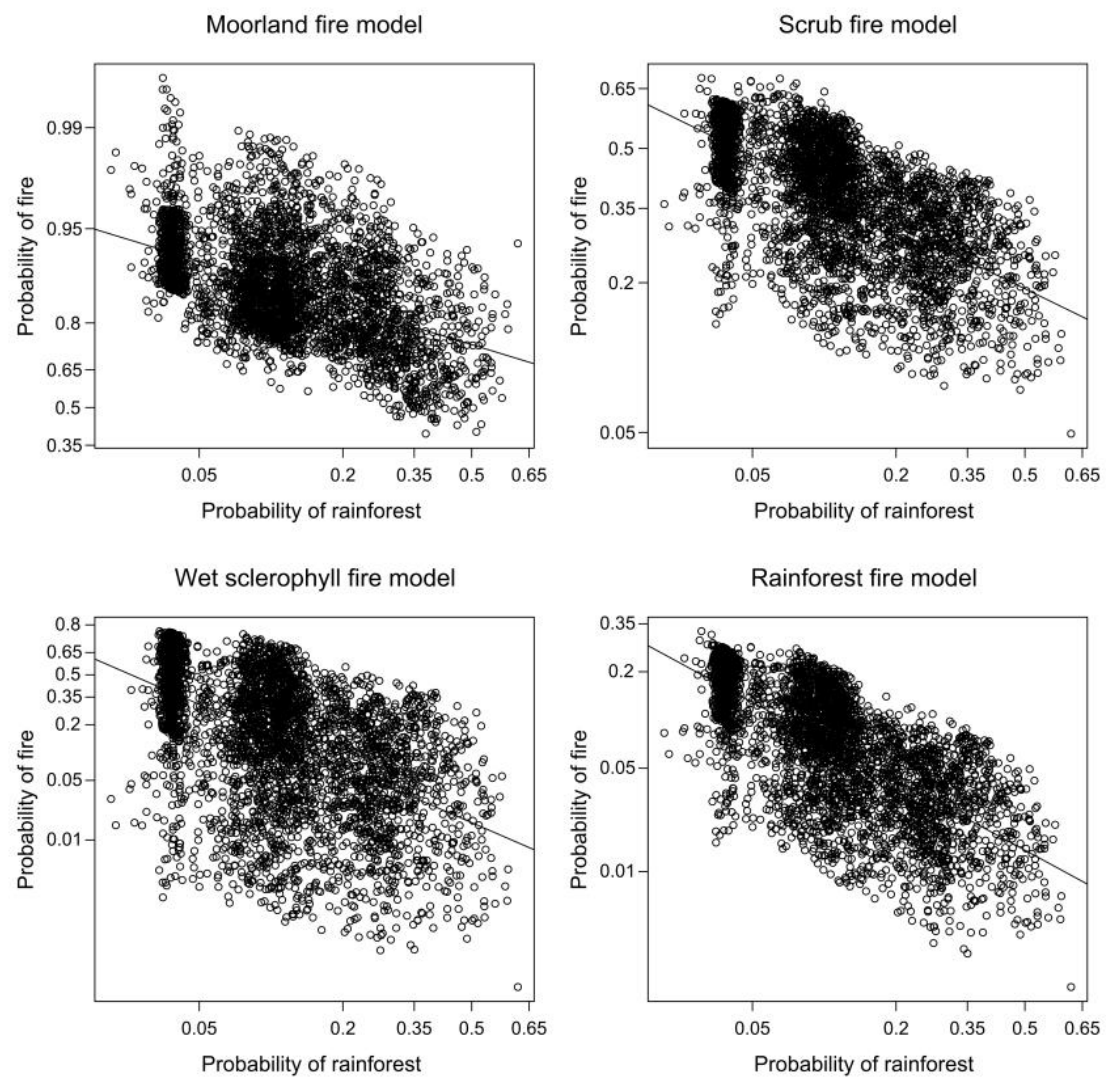


Figure 2.7. The relationship between the predicted probability of rainforest and the predicted probability of fire for 4200 random points in the landscape, calculated separately using the selected model for rainforest distribution (see Table 2.3, Figure 2.4) and the selected models for fire occurrence in moorland, scrub, wet sclerophyll and rainforest (see Table 2.3, Figure 2.6). Axes are on a logit scale, with probability values shown. A least squares regression line was fitted to the data. Note the difference in y-axis scales across vegetation types, which is a reflection of their relative flammability.

Discussion

Rainforests and fire refugia

Our results indicated that rainforest on nutrient-poor substrates in southwest Tasmania is most likely to be found in valleys and on steep south-facing slopes, and least likely to be found on flats, ridges and steep north-facing slopes. The four fires we analysed typically burnt within treeless moorlands and stopped on boundaries with surrounding less flammable woody vegetation types. In all four vegetation types, fires were most likely to burn on flats, ridges and steep north-facing slopes and least likely to burn in valleys and on steep south-facing slopes. Our results suggest an antagonism between fire and rainforest, whereby rainforest preferentially occupies parts of the landscape where fire is least likely to burn. This supports the long-held – but previously untested – hypothesis that the distribution of rainforest in southwest Tasmania is related to topographic fire refugia (Casson, 1952; Gilbert, 1959; Jackson, 1968; Mount, 1979; Brown and Podger, 1982a; Read, 1999; Brown *et al.*, 2002). It is important to note that our analyses were constrained to the nutrient-poor substrates that dominate southwest Tasmania and form the basis for the Jackson (1968) model. It is likely that other environmental factors such as geology, soil type and drainage play a role in determining the distribution of rainforest in southwest Tasmania (i.e. Mount, 1979) and these could be integrated into our modelling framework (see Murphy *et al.*, 2010) once higher resolution maps become available.

Correlative studies that analyse the relationship between the occurrence of spatially restricted vegetation types and terrain characteristics derived from digital elevation models (e.g. Brook and Bowman, 2006; Coblenz and Keating, 2008) or field-based measurements (e.g. Ash, 1988; Fensham, 1995; Lindenmayer *et al.*, 2000a) have led to a wide acceptance of the role

of topographic fire refugia in many fire-prone landscapes in Australia (reviewed by Bowman, 2000) and other parts of the world (Geldenhuys, 1994; Bond and van Wilgen, 1996; Perry and Enright, 2002; Coblenz and Keating, 2008). In these studies, the mechanistic link between particular topographic locations occupied by rainforest and topographic fire refugia has been largely inferential. By analysing the pattern of fire scars in the landscape, we were able to take the next step to explicitly describe which parts of the landscape actually constitute fire refugia and make the statistical association with rainforest distribution. We do not dispute the conclusions made in previous studies that have not incorporated independent fire data. In fact, our results probably corroborate their conclusions given that most of these previous studies identify similar terrain attributes (i.e. steep valleys and particular slopes or aspects) to those shown to be topographic fire refugia in southwest Tasmania. However, we argue that future investigations into the role of topographic fire refugia would benefit from adopting the more rigorous analytic framework developed here, particularly with the increasing availability of high resolution remote sensing products (Hoy *et al.*, 2008) and recent progress in analysing spatially autocorrelated data (Dormann *et al.*, 2007; Murphy *et al.*, 2010).

Flammability of vegetation communities

The pattern of fire in the landscape was clearly influenced by the flammability of the broad vegetation communities in southwest Tasmania (Pyrke and Marsden-Smedley, 2005). Moorlands were by far the most extensively burnt vegetation type, which is consistent with the exceptionally high flammability of this vegetation community (Marsden-Smedley and Catchpole, 1995a,b). In general, fires tended to extinguish when they encountered less flammable vegetation types, with the unburnt buffer around the perimeter of each fire (including 'islands' of unburnt vegetation within the fire scars) comprised mostly wet

sclerophyll or rainforest vegetation. Indeed, only 6% of the total area burnt by the fires we mapped was rainforest (Table 2.2) – a figure consistent with that reported by Marsden-Smedley and Kirkpatrick (2000), who estimated that rainforest accounted for only 6% of the total area burnt by fires in southwest Tasmania as mapped from aerial photographs between 1940 and 2000. The relative flammability of the four vegetation types is neatly summarized by the ratio of burnt and unburnt points calculated for each vegetation community in this study (moorland > scrub > wet sclerophyll > rainforest, Figure 2.5c). This hierarchy of flammability across vegetation types at the landscape scale matches the hierarchy of assumed mean fire frequencies (moorland > scrub > wet sclerophyll > rainforest) that underpin the ecological models proposed for this region (Jackson, 1968; Mount, 1979). It should be noted that the flammability of forest within the landscape vegetation matrix will also be a function of its proximity to moorland and this was not taken into account in these calculations of flammability.

Fire and topography

Our modelling showed that topographic position, aspect and elevation were all important factors in explaining the occurrence of fire in the landscape (see Figure 2.6). Importantly, the modelled relationships between these topographic factors and fire occurrence were remarkably consistent for all four vegetation types. Most studies of the influence of topography on satellite-mapped burnt area or burn severity conclude that the pattern of fire in the landscape is not due to topography *per se*, but it is the topographic position in relation to fire weather and the direction of fire movement that dictates fire spread (e.g. Alexander *et al.*, 2006; Collins *et al.*, 2007; Lee *et al.*, 2009; Oliveras *et al.*, 2009; Viedma *et al.*, 2009; Bradstock *et al.*, 2010). For this reason, our finding that north-facing slopes had a higher probability of burning than southern slopes is not surprising. The prevailing winds during the

fires we analysed were north to north-westerly, resulting in the preferential burning of windward north-facing slopes compared to leeward south-facing slopes. Further studies of similar landscape scale fires (as they arise in the future) are required to detect the effect of variable fire weather on fire spread. Indeed, using similar logic to this study, Geldenhuys (1994) demonstrated that these interactions between prevailing fire winds and terrain physiography strongly influence the location pattern of fire-sensitive forest patches in an analogous southern South African firescape. The effect of aspect may be exacerbated by the tendency for fuel loads to be drier on northerly aspects in southwest Tasmania (Marsden-Smedley and Catchpole, 2001) due to increased exposure to solar radiation compared to southerly aspects. We also found that the probability of fire was lowest in valleys and highest on ridges and flats. In a satellite-mapped fire scar analysis in the topographically complex Blue Mountains region of south-eastern Australia, Bradstock *et al.* (2010) also found that there was a higher predicted probability of crown fires on ridges than in valleys. We agree with Bradstock *et al.* (2010), that this trend is probably due to a declining exposure to wind from ridgetops to valleys and a concomitant increase in fuel moisture content.

Fire, topography and alternative stable state models

Our data strongly suggest that tests of fire-mediated alternative stable vegetation states in topographically complex landscapes should include the effect of local topographic features (i.e. slope, aspect, topographic position) on fire–vegetation feedbacks. As suggested by Jackson (1968) and Mount (1979), the overarching control exerted by topography on fire–vegetation feedback loops comprises an added degree of resilience within the various vegetation communities and thus clearly influences the state-transition dynamics in southwest Tasmania. These interactions are likely to apply to other mountainous landscapes thought to contain fire-mediated alternative stable vegetation communities (e.g. Petraitis and Latham,

1999; Perry and Enright, 2002; Warman and Moles, 2009; Odion *et al.*, 2010), although the direction of the relationships between topography, vegetation and fire would almost certainly vary from system to system and the strength of the relationships would probably decrease in more topographically benign landscapes (e.g. Murphy *et al.*, 2010). Understanding these interactions is crucial given that increased temperatures under climatic change may result in drier forest fuels. This could result in the further contraction of rainforests into topographic refugia (i.e. Australian monsoon tropics: Brook and Bowman, 2006) due to increased incursions by fire, and reduced growth and recovery rates of rainforest trees.

Whether or not the added resilience provided by topography is strong enough to prevent vegetation state transitions in Tasmania (i.e. Jackson, 1968 or Mount, 1979, respectively) remains unresolved. Evaluating the efficacy of the alternative stable state model (Jackson, 1968) or the ‘stable fire cycles’ model of Mount (1979) for southwest Tasmanian landscapes requires datasets with a high temporal resolution (Petraitis and Latham, 1999), which our study of a few fire events and the distribution of rainforests at a single point in time cannot provide. Recent palaeoecological studies have shown that the pattern of lowland vegetation has remained remarkably stable throughout the Holocene (Fletcher and Thomas, 2007a, 2010b), with the authors suggesting the apparent resilience of each vegetation community is the result of fire–vegetation feedbacks that were maintained by Aboriginal burning throughout this period (Fletcher and Thomas, 2010a). Unfortunately, the low spatial resolution of these studies precludes any detailed analysis of the role of environmental variables such as topography in influencing this apparent stability. Targeted studies of temporal series of aerial photography (e.g. Banfai and Bowman, 2006; Lehmann *et al.*, 2009) to detect vegetation transition trajectories and correlating these changes with fire history and environmental gradients (e.g. Petraitis and Latham, 1999; Brook and Bowman, 2006) may be

a useful approach in southwest Tasmania to clarify the mechanisms behind various pathways of change.

Conclusions

The occurrence of *Nothofagus*-dominated temperate rainforest on nutrient-poor substrates in the archetypical ‘firescape’ of southwest Tasmania is clearly related to parts of the landscape terrain that are protected from fire. Therefore, we confirm the long-held – but previously untested – hypothesis that topographic fire refugia provide the underlying mechanism controlling rainforest distribution in this region. Unlike previous studies of topographic fire refugia, our analytical framework incorporated both the relationship between topography and rainforest, and the relationship between topography and fire, thus allowing us to demonstrate explicitly that rainforest was indeed confined to topographic positions where fire was least likely to go. Whilst our study lacked the temporal resolution required to resolve the debate between the Jackson (1968) and Mount (1979) ecological models proposed for the region, our results corroborate the fire–vegetation–topography interactions that underpin these models. As such, we suggest that topography should be included in tests of the efficacy of fire-mediated alternative stable state models in other fire-prone landscapes.

Chapter 3: Alternative stable states and the role of fire-vegetation-soil feedbacks in the temperate wilderness of southwest Tasmania

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Abstract

Two ecological models have been put forward to explain the dynamics of fire-promoting and fire-sensitive vegetation in southwest Tasmania: the alternative stable states model of Jackson (1968) and the sharpening switch model of Mount (1979). Assessing the efficacy of these models requires high resolution spatio-temporal data on whether vegetation patterns are stable or dynamic across landscapes. We analysed ortho-rectified sequences of aerial photography and satellite imagery from 1948, 1988 and 2010 to detect decadal scale changes in forest and non-forest vegetation cover in southwest Tasmania. There was negligible change from forest to non-forest ($<0.05\%$) and only a modest change from non-forest to forest over the study period. Forest cover increased by 4.1% between 1948 and 1988, apparently due to the recovery of forest vegetation following stand-replacing fire prior to 1948. Forest cover increased by 0.8% between 1988 and 2010, reflecting the limited ability of forest to invade treeless areas. The two models include interactions between vegetation, fire and soil, which we investigated by analysing the chemical (phosphorus, nitrogen) and physical properties (clay, silt) of 128 soil samples collected across 34 forest – non-forest boundaries. Phosphorus in the upper horizon was typically lower in non-forest vegetation compared to forest vegetation, which is consistent with proposed fire-vegetation-soil feedbacks. Mineral horizons were dominated by sand, with low levels of clay under all vegetation types. Available field evidence lends support to the Jackson (1968) alternative stable states model as the most suitable model of vegetation dynamics on nutrient poor substrates in southwest Tasmania although modifications of the timeframes for transitions toward rainforest are required.

Introduction

Mosaics of fire-resistant and fire-prone vegetation within the same environmental settings have long fascinated ecologists (Mutch, 1970; Geldenhuys, 1994; Bowman, 2000; Bond *et al.*, 2005). There has been a recent surge of interest in whether a range of coexisting terrestrial vegetation communities persist as alternative stable states that are maintained by fire (Hoffmann *et al.*, 2009; Warman and Moles, 2009; Odion *et al.*, 2010; Lehmann *et al.*, 2011; Staver *et al.*, 2011). Across flammable landscapes, alternative stable state theory predicts that a complex suite of feedbacks between fire, vegetation and other environmental variables act to maintain coexisting vegetation communities through time (Wilson and Agnew, 1992) and that the breakdown of these feedbacks may result in relatively rapid transitions between otherwise stable states (Petraitis and Latham, 1999; Scheffer *et al.*, 2001).

One of the earliest examples of an alternative stable states model for landscapes experiencing periodic fire was put forward by Jackson (1968; see also Bowman and Jackson, 1981) to explain ‘islands’ of relatively fire resistant forest amongst frequently burnt moorland and heath communities in the southwest of Australia’s island state, Tasmania (Wood *et al.*, 2011a). In his ‘ecological drift’ model Jackson (1968) argued that each vegetation community in southwest Tasmania actively modifies the rate of fuel accumulation and fuel characteristics (and therefore fire frequency), soil nutrient capital and light environment in a direction that enhances its own growth and survival, and simultaneously hinders or constrains other vegetation types (Figure 3.1). Jackson (1968) suggested that these positive feedbacks engender an inherent resilience to vegetation change, but also included the possibility that highly improbable deviations from average fire frequencies can push an otherwise stable vegetation community beyond its ‘resilience threshold’ and cause a transition to an alternative vegetation community (Figure 3.1).

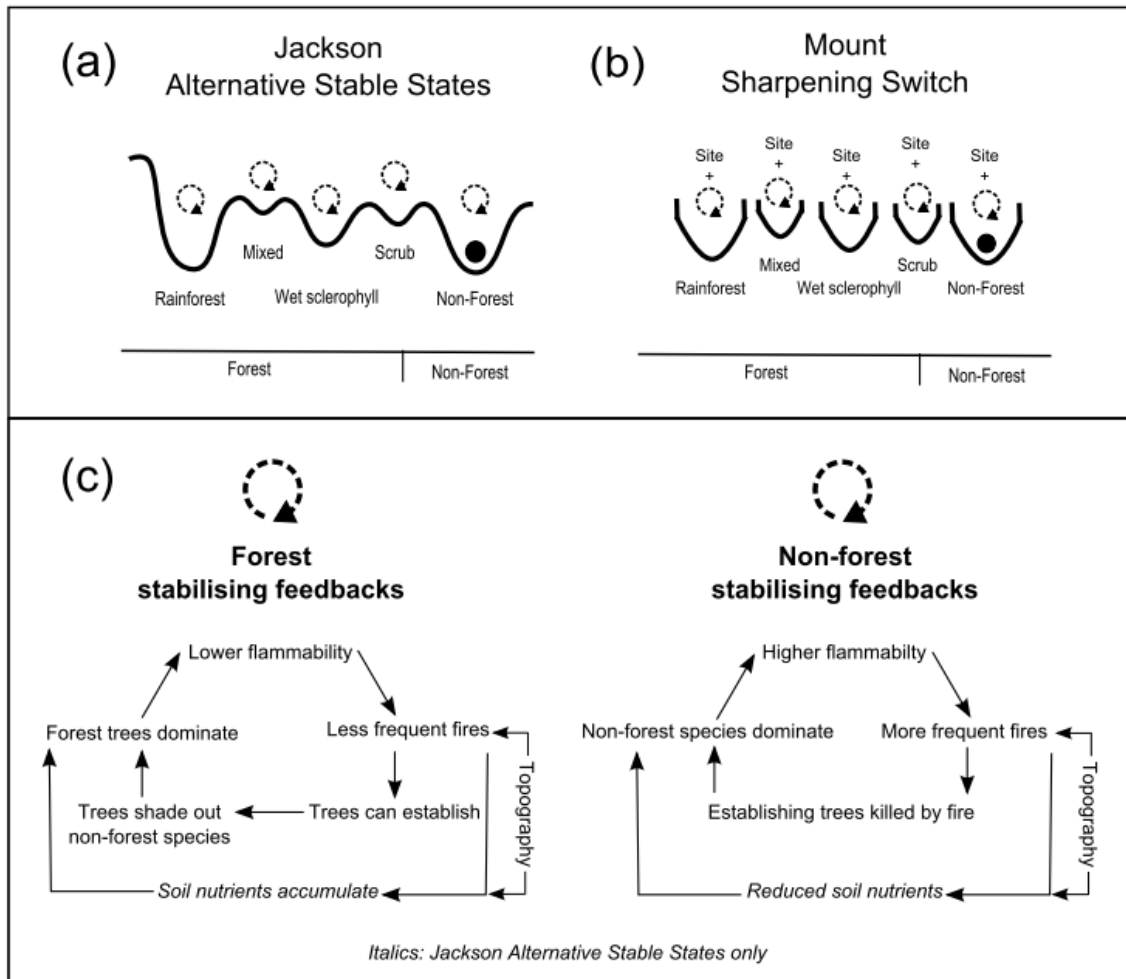


Figure 3.1: Models of vegetation dynamics for southwest Tasmania illustrated with the ‘ball and cup’ heuristic model commonly used to describe alternative stable states (see Scheffer *et al.*, 2001; Warman and Moles, 2009). (a) In Jackson’s (1968) ‘alternative stable states’ model each vegetation community can occupy any underlying physical environmental setting. Each potential vegetation state is determined by fire-vegetation-soil feedbacks [see (c)] and the cumulative effect of these feedbacks is represented by resilient ‘basins of attraction’. A vegetation community - represented by the ball – will resist disturbance by fire initially and return to the original state, but if pushed beyond the threshold by repeated stand replacing fire (or lack thereof), positive feedbacks from the neighbouring stable state will take over and the system will undergo a transition to another stable state. (b) In Mount’s (1979) ‘sharpening switch’ model each vegetation community is initially determined by the underlying physical environment (or ‘site’, *sensu* Mount 1979). Feedback mechanisms between fire and vegetation [see (c)] reinforce these patterns by creating deeper ‘basins of attraction’. The resilience created by these feedbacks is strong enough to prevent vegetation state transitions creating stable vegetation patterns. (c) Conceptual model showing the stabilising feedbacks that maintain the forest and non-forest vegetation states investigated in this study. Adapted from Petraitis and Latham (1999).

Mount (1979) proposed an alternative model for southwest Tasmania that underscores the importance of site characteristics and predicts geographically static vegetation patterns (Figure 3.1). This so-called ‘stable fire cycles’ model is effectively a ‘one-factor sharpening switch’ (*sensu* Wilson and Agnew 1992) where fire merely reinforces environmentally determined vegetation patterns. Whilst Jackson’s alternative stable states model allows for vegetation state transitions, Mount’s model suggests that the positive feedbacks between fire and vegetation are strong enough to eliminate vegetation state transitions and that physical environmental factors exert significant control over vegetation patterns. Accordingly, fire alone does not determine vegetation; rather, the risk of fire is determined by vegetation, which in turn, is related to ‘site factors’ in the landscape (i.e. geology, drainage, topography).

Testing the efficacy of these competing models - and alternative stable states models in general – requires multiple lines of ecological evidence collected at a range of appropriate temporal and spatial scales (Petraitis and Latham, 1999; Thomas *et al.*, 2010). In southwest Tasmania there has been a multitude of millennial scale palaeoecological studies (reviewed by Thomas *et al.*, 2010) which have traditionally favoured scenarios of fluctuating vegetation patterns in response to Quaternary climate change (Macphail, 1979; Colhoun, 1996). However, Fletcher and Thomas (2007, 2010a) recently posited largely stable vegetation patterns throughout the Holocene, arguing that moorland and rainforest was held in place by regular aboriginal burning and underlying edaphic features in the landscape. These palynological studies are necessarily limited in their spatial resolution and cannot detect short-term shifts in vegetation boundaries; a problem that could not be overcome using stable carbon isotopes in the organic soils of the region (Wood *et al.*, 2011b). Studies in the region focussing on shorter temporal scales are limited to a spatially restricted set of monitoring plots which showed negligible shifts in boundaries between structural types in southwest Tasmania over a 20 year period (Brown *et al.*, 2002). Thus the historical context for

understanding the dynamics of this region remains limited and ecologists have relied on modelling (Henderson and Wilkins, 1975; King *et al.*, 2006) and space-for-time chronosequences (Brown and Podger, 1982; Bowman *et al.*, 1986) to infer vegetation dynamics and engender a general acceptance of the Jackson (1968) alternative stable states model (Bowman and Wood, 2009). The question remains: are forest boundaries stable or shifting over decadal to century scales? If so, what are the environmental drivers of these dynamics and are they related to feedback mechanisms that act to maintain alternative stable vegetation communities?

We used sequences of remotely sensed images to investigate decadal scale dynamics of forest and non-forest vegetation communities in southwest Tasmania. Analysis of historical sequences of aerial photographs and satellite images have provided invaluable ‘snapshots’ of change in vegetative cover since the 1940’s (reviewed by Fensham and Fairfax, 2002) and have been particularly powerful in detecting often surprising savannah and rainforest dynamics in Northern Australia (reviewed by Bowman *et al.*, 2010). When combined with spatially explicit data on disturbance regimes (i.e. fire, herbivory) and resource availability (i.e. rainfall, soil type) these maps of vegetation change can unlock the mechanisms driving vegetation dynamics in the landscape (e.g. Brook and Bowman, 2006; Banfai *et al.*, 2007). In this study we used aerial photographs and high resolution satellite imagery from 1948, 1988 and 2010 to document the dynamics of forest and non-forest vegetation cover over 62 years for a ~60,000 ha region in remote southwest Tasmania. We then linked these observed dynamics with available spatial proxies for fire spread (Wood *et al.*, 2011a) to investigate some of the key concepts proposed by Jackson (1968) and Mount (1979).

A second aim of our study was to investigate whether the chemical and physical properties of soils in forest and non-forest communities have the potential to influence vegetation dynamics. Jackson (1968, 2000) proposed feedbacks between vegetation, fire and the regions

unique organic soils that act to further stabilise vegetation communities (Figure 3.1). Frequent fires in flammable vegetation communities are hypothesised to deplete nutrient stocks to an extent that impedes the development of forest vegetation (see Bond, 2010) and – in contrast - rarely burnt forest vegetation has the potential to accumulate nutrients in its biomass and underlying organic soils enabling rapid post-fire recovery of forest vegetation. Similar feedbacks invoking soil characteristics are discussed for other vegetation mosaics purported to function as fire-mediated alternative stable states (Perry and Enright, 2002; Hoffmann *et al.*, 2009; Murphy *et al.*, 2010; Odion *et al.*, 2010). Field studies have found disparities in nitrogen and phosphorus in organic soils between forest and non-forest vegetation across three boundaries in southwest Tasmania (Bowman *et al.*, 1986; Wood *et al.*, 2011b), but the generality of these results across the landscape is yet to be tested. Further, Pemberton (1989) and di Folco (2007) noted that forest and rainforest vegetation in southwest Tasmania may be associated with sites with relatively clay rich mineral soils, which, if true, would lend support to Mount's (1979) emphasis on physical environmental variables such geology and its constituent soils exerting significant controls on vegetation patterns. We collected soil samples from organic and mineral soil horizons to test whether soil characteristics (phosphorus, nitrogen, clay and silt) differ across forest - non-forest boundaries.

Methods

Study Area

The study was focused on the remote Melaleuca region (Figure 3.2) in southwest Tasmania - an area that is conserved as part of the Tasmanian Wilderness World Heritage Area. The regional climate is classified as perihumid cool (Gentilli, 1972) with an average annual

rainfall at Melaleuca of approximately 2400mm (Brown and Podger, 1982). Approximate mean winter and summer minimum and maximum temperatures are 3 and 10 °C, and 10 and 20 °C respectively. Infertile Precambrian metamorphic rocks dominate the region's geology (Pemberton, 1989). Multiple glaciations during the Quaternary have created a terrain characterised by rugged mountains emergent from broad terraced plains of glacial outwash (Macphail *et al.*, 1999). Lowland vegetation throughout southwest Tasmania forms a mosaic of treeless heath-moorland, sclerophyllous scrub, eucalypt forest and rainforest vegetation with shallow to deep organic soils forming under all vegetation types (Wood *et al.*, 2011b). Aboriginal occupation in the region stretched back to 35,000 years BP which provided an ignition source to the region that was independent of climate (Fletcher and Thomas, 2010a). European colonisation caused the expatriation of the Aboriginal tribes and the creation of a wilderness, except for localised small-scale tin mining operations at Melaleuca and Coxes Bight (Figure 3.2). Humans remain the predominant ignition source of wildfires, although lightning is known to start fires. Fire maps of the study area (Marsden-Smedley, 1998) suggest that almost two thirds of the study area were affected by a wildfire in 1933/34 which burned over 600,000 ha of southwest Tasmania (Marsden Smedley and Kirkpatrick, 2000).

Landscape analyses

Repeat image analysis of vegetation dynamics 1948-2010

Digitised aerial photographs from 1948 (black and white; 1:16000) and 1988 (colour; 1:25000), and an 0.5m resolution panchromatic World-View 2 satellite image from 2010 were analysed to assess vegetation cover. Ortho-rectified mosaics of 1948, 1988 and 2010 imagery covering the study area were created using the ortho-photography software Landscape Mapper (Myriax Software Pty Ltd, Hobart: <http://www.myriax.com>). A comprehensive landscape wide analysis of these image-mosaics was not possible because of localised regions

of blurred 1948 imagery or misaligned image sequences, particularly on photo-mosaic joins. Instead we focussed our analysis on a series of sixty-seven 600m x 600m sample areas distributed randomly across parts of the landscape that did not coincide with a) overtly blurred 1948 imagery, b) an image-mosaic join or c) a ~3km buffer around the tin-mining areas at Melaleuca and Coxes Bight (Figure 3.2). At each sample area, the 1948, 1988 and 2010 images were clipped to the 600m x 600m squares and overlaid within ArcGIS10, where obvious misalignments were corrected using the spline function in the ArcGIS10 Georeferencing Toolbox.

A 30 x 30 grid of 20 m² cells (n=900) were overlaid onto each sample area and the vegetation of each cell was manually classified for 1948, 1988 and 2010 at a common scale of 1:2500 (Figure 3.2). We used a classification scheme of ‘treeless moorland and low scrub’ (herein, ‘non-forest’, NF) and ‘tall scrub and forest with trees’ (herein, ‘forest’, F) based on the presence of tree canopies occupying >50% of the cell. More detailed classification systems were prohibited by the quality of the 1948 aerial photographs and the resolution of the 1988 aerial photographs. These classifications were necessarily subjective and consequently only one of us (SW) conducted this task. The accuracy of our classification was assessed using the GPS location of assessments of vegetation type (i.e. forest or non-forest) made at 169 points collected during the field survey of soils described below. Our sampling design appeared to be representative of the wider landscape given that the proportional area classified as forest in our sampled areas in 1988 (Figure 3.2; ~2304ha; 31.2%) compares well with the proportion of forest calculated from the TASVEG mapping product for the Melaleuca Study Area (Figure 3.2; ~65000ha; 31.9%) and the nutrient poor substrates of southwest Tasmania (Wood *et al.*, 2011a; ~540,000 ha; 34.3%).

To examine the dynamics of individual cells, we calculated the percentage of forested (F) and non-forested (NF) cells that changed (i.e. F-NF or NF-F) or remained stable (i.e. F-F, NF-NF) between the two time periods (1948-1988 and 1988-2010). For all cells that changed from non-forest to forest (NF-F), we calculated the distance to the nearest forest (F) cell in each 1948 grid using the Spatial Join tool in ArcGIS10. The total area – in hectares - of forest (F) and non-forest (NF) vegetation in our sampled area was calculated based on each cell being 0.4ha. This information was used to calculate statistics for vegetation cover and vegetation cover change over time.

Testing the effect of fire on vegetation dynamics

We used two proxies for fire to investigate the effect of fire on observed boundary dynamics from the repeat image analysis. Firstly, we used digitised maps of fires (Marsden-Smedley, 1998) to provide a broad-scale understanding of fire activity in our study area. Using these maps, each cell in our sampled area was attributed with the presence/absence of fire for the 20-22 year periods 1928-1948, 1948-1968, 1968-1988 and 1988-2010. The coarse spatial resolution of these fire maps precluded detailed spatial analysis.

Secondly, we adopted the modelling framework of Wood *et al.*, (2011a) to test whether parts of the landscape that changed from non-forest (NF) to forest (F) were likely to be the result of regeneration of forest after a stand-replacing fire. In an analysis of patterns of fire spread, Wood *et al.*, (2011a) showed that fire in southwest Tasmania preferentially burns particular parts of the landscape terrain – namely, ridges and flats but not valleys; and steep northern slopes but not steep southern slopes. We hypothesised that if parts of the landscape that changed from non-forest to forest show the same relationships with topography as those observed between fire and topography, then it is likely that this change is associated with the regrowth of forest canopies following stand-replacing fire.

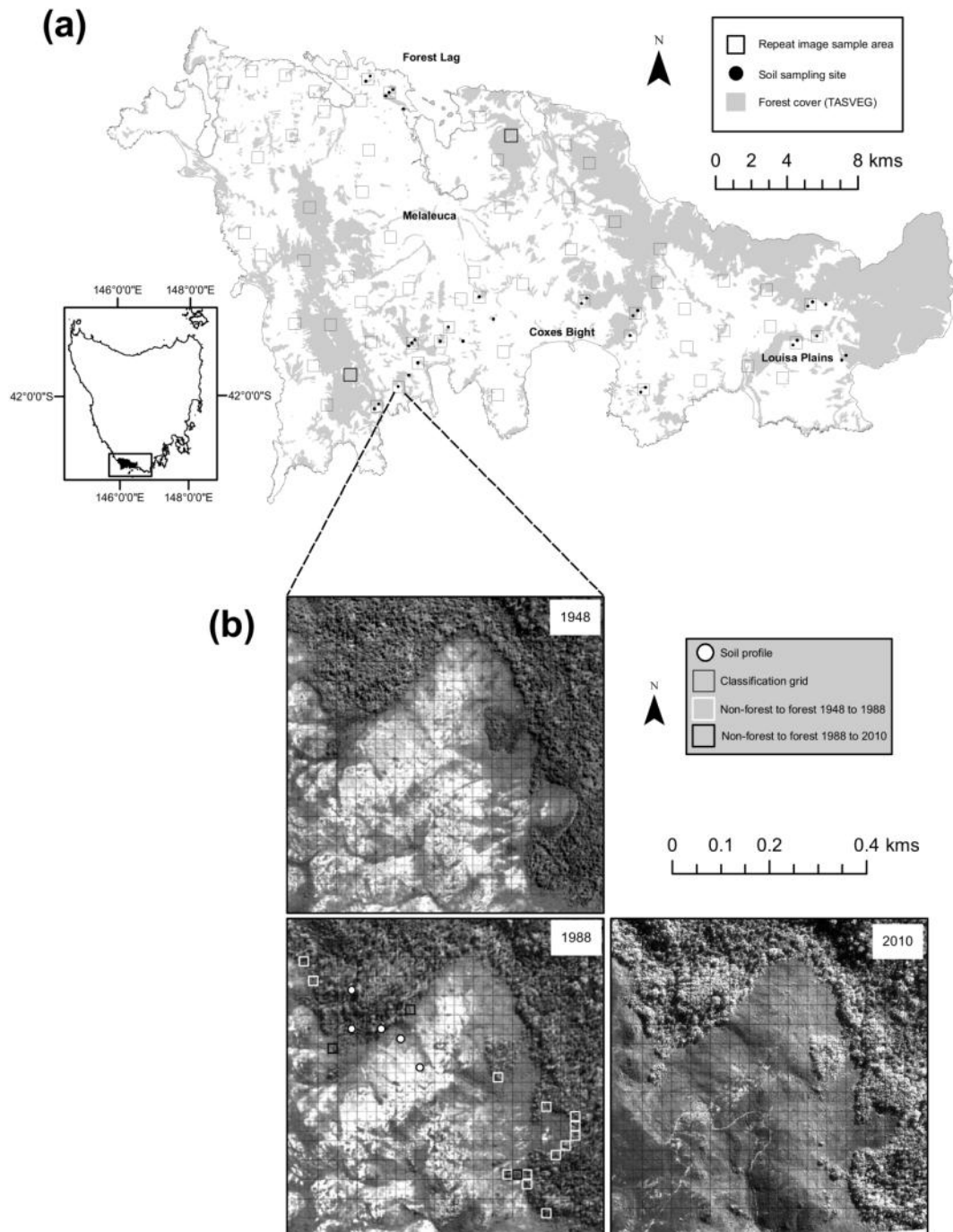


Figure 3.2. (a) Map of Melaleuca Study Area in southwest Tasmania showing the extent of forest cover (31.9%: Harris and Kitchener, 2005), the location of sixty-seven sample grids used in repeat image analysis and the location of soil sampling transects. (b) An example of repeat image analysis using aerial photography (1948 and 1988) and satellite imagery (2010). At this location the area of forest increased by 4.0% between 1948 and 1988 and then 0.9% from 1988 to 2010. Soil profiles for this sample area are also shown.

We randomly selected 4000 cells that were classified as forest in 1988 and attributed each cell with a presence/absence of non-forest to forest change (NF-F) between 1948 and 1988. Each cell was also assigned three topographic attributes derived from a digital elevation model (topographic position, northness index, elevation; see Chapter 2). The same cell attribution process was repeated for cells that changed from non-forest to forest (NF-F) between 1988 and 2010. All combinations, without interactions, of the three topographic variables considered important correlates of non-forest to forest conversion were constructed in generalised autoregressive error (GAR_{err}) models (Murphy *et al.*, 2010; Wood *et al.*, 2011a). This type of model has been recently developed by Murphy *et al.*, (2010) to analyse spatially autocorellated non-normal data. It is analogous to the simultaneous autoregressive error model for normal data (Cressie, 1993), but can cope with non normal data types in the same way as a generalised linear model. All statistical analysis was done with R (v.2.12; R Foundation for Statistical Computing, Vienna, Austria).

Change from non-forest to forest represented presense/absence data and was modelled using binomial errors. Models were evaluated using a robust form of Akaike's Information Criterion, AIC_c, a model selection index favouring both model fit and model simplicity (Burnham and Anderson, 2002). Lower values of AIC_c indicate greater support for a model, relative to other models in the same candidate set. From AIC_c, Akaike weights (w_i) were calculated for each model, and these are equivalent to the probability of a given model being the best in the candidate set. The importance of each variable was evaluated by calculating w_+ , the sum of w_i for all models in which that variable occurred. For each variable, w_+ is equivalent to the probability of the best model containing that variable, and is a useful expression of the weight of evidence for the importance of the variable. We considered that w_+ values of <0.73 were indicative of substantial model selection uncertainty. A w_+ value of 0.73 is equivalent to an AIC_c difference of two units between models containing the variable

under examination and those not containing it. An AIC_c difference of two units is a common ‘rule of thumb’ used by ecologists to assess clear evidence of an effect (Richards, 2005).

Soil characteristics of forest and non-forest vegetation

Soil sampling

We established thirty-four transects across forest boundaries prior to our repeat image analysis, with locations and boundary delineation based on existing vegetation mapping from 1:25,000 aerial photography (TASVEG: Harris and Kitchener, 2005). Vegetation change trajectories and the distance to the forest boundary for each soil profile were subsequently determined using data from the repeat image analysis described above. On each transect we dug five soil profiles - three in forest and two in non-forest - and recorded the location in a GPS (Figure 3.2). The ‘forest’ soil profiles were situated in rainforest, mixed eucalypt-rainforest or sclerophyll forest > 5m tall. The ‘non-forest’ profiles were situated in treeless moorlands dominated by buttongrass (*Gymnoschoenus sphaerocephalus*) with or without a low (< 2m) heathy scrub component. Topographic position was classified into valley, ridge, valley flat, upper, mid and lower slope. Soil pits were dug down to the regolith, rocky substrate or an impenetrable gravel layer. The depth of the organic and mineral layers were measured and the organic layer classified to a simplified von Post scale (i.e. sapric, hemic or fibric in decreasing order of organic matter decomposition; Isbell, 2002). We collected samples from the upper 10cm (usually organic, but sometimes mineral) and from the lowest distinguishable soil horizon (usually mineral but sometimes organic).

Lab Methods

The organic content of all soil samples from the upper and lower horizons was derived by loss on ignition, where 5-10 g samples were combusted at 550 °C for 6 hours. Given our statistical design (see below) we conducted our analyses only on soil profiles that included a distinct mineral horizon (i.e. lower profile organic content <20%; Isbell, 2002). Soil samples from the upper 10cm were ground to powder in a Retsch MM200 ball mill (MEP Instruments Australia, North Ryde, Australia) and analysed for total phosphorus and total nitrogen. For phosphorus analysis, ground soil samples were dried at 70 °C for 24 hours, finely ground, and digested in concentrated sulphuric acid on an open block digester. Total phosphorus concentrations were determined colorimetrically using a modified ascorbic acid method (Kuo, 1996). Soil samples were analysed for nitrogen concentration on a Perkin Elmer 2400 Series II elemental analyser (Analytical Development Company, Adelaide, Australia). We conducted a particle size analysis on all soil samples from the lower profile using a hydrometer to determine the percent sand (0.2mm), silt (0.02mm) and clay (0.002mm) (Australian Standard AS1289.3.6.30). All samples were pre-treated with hydrogen peroxide to remove organic matter.

Statistical Analysis

We evaluated the importance of four soil variables in explaining differences in vegetation across forest - non-forest boundaries: (1) total phosphorus and (2) total nitrogen in the upper horizon; and (3) percent clay and (4) percent silt in the lower horizon. Drawing on the fire-vegetation-soil interactions outlined in Figure 3.1, we hypothesised that phosphorus and nitrogen would be higher in forest vegetation compared to non-forested vegetation (Jackson, 1968; Bowman *et al.*, 1986; di Folco, 2007; Wood *et al.*, 2011b) and that forest vegetation

would preferentially occupy sites with finer textured soils (Mount, 1979; Pemberton, 1989; di Folco, 2007).

Topography is a key driver of soil processes in southwest Tasmania (Wood *et al.*, 2011b), with topographic position (i.e. basin, slope, shelf) influencing the effects of fire and drainage on soil accumulation and carbon dynamics in the region (di Folco and Kirkpatrick, 2011). We followed the logic of di Folco and Kirkpatrick (2011) and divided our dataset into two topographic classes: (1) soil profiles from ‘run-off’ topographic positions such as ridges, mid slopes and upper slopes; and (2) soil profiles from ‘run-on’ topographic positions such as valleys, valley flats and footslopes. For each of these two datasets, models representing all combinations of the four soil response variables, without interactions, were constructed as linear mixed effects models and analysed using the lme4 package (Bates *et al.*, 2008) in R (v.2.12; R Foundation for Statistical Computing, Vienna, Austria). Mixed effects models allowed us to account for the correlation between soil variables located on the same transect. The vegetation type (forest or non-forest) explanatory variable was considered on the basis of the presence/absence of forest and was modelled using binomial errors. Models and response variables were evaluated using the same approach outlined above (i.e. AIC_c and w₊). Finally, we examined the relationship between total phosphorus and distance from the forest boundary.

Results

Repeat image analysis of vegetation dynamics

There was a strong concordance between our image classification and field classified vegetation types, with the correct image classification of 163 of 169 (97%) field surveyed

points. The vast majority of cells classified as non-forest (NF) or forest (F) remained the same through time (NF-NF, F-F), with negligible change from forest to non-forest (F-NF) but a modest amount of change from non-forest into forest (NF-F; Figure 3.3). The total area of forest in our sampled area (2304 ha) increased from 700 ha (29.9%) in 1948 to 729 ha (31.2%) in 1988 to 735 ha (31.4%) in 2010. The proportional change in forest area (relative to the initial forest coverage on the earliest image) differed for the two time periods with a 4.1% increase in forest area from 1948 to 1988 and a 0.8% increase in forest area from 1988 to 2010. Most areas transitioning from non-forest to forest were situated within 20 m of the forest boundary (Figure 3.4).

Assessment of broad scale fire maps (Marsden-Smedley, 1998) revealed a decline in fire activity in our sampled area. The proportion of repeat image analysis sample cells burnt for each time period examined was 61% (1928-1948, all in summer 1933/34), 3% (1948-1968), 3% (1968-1988) and 12% (1988-2010). There were no topographic variables that were strongly correlated with cells that changed from non-forest to forest from 1988 to 2010 (Table 3.1). However, modelling showed that cells that changed from non-forest to forest between 1948 and 1988 were clearly correlated with topographic position and northness index (Table 3.1). According to the selected model, the increase in forest area from 1948 to 1988 was more likely to occur on flats, gentle slopes and ridges, but not valleys; and steep northern slopes compared with steep southern slopes (Figure 3.5a).

Soil characteristics of forest and non-forest vegetation

Of the 169 soil profiles, 41 lacked a mineral horizon and were excluded giving us a final dataset of 128 soil profiles (Table 3.2). Examination of the 1948, 1988 and 2010 photo sequences revealed that vegetation at all 128 soil profiles has remained stable for the past 62

years. In general, the forested profiles were dominated by shallow to deep fibric upper horizons whereas the non-forest profiles were dominated by shallow to deep sapric and hemic upper horizons (Table 3.2). The lower horizons of both forest and non-forest soils were dominated by sand, with clays present in only small amounts (Table 3.2). Model selection ($w+$) suggested that the contrast between forest and non-forest vegetation was strongly correlated with total phosphorus on all topographies and percent clay on slopes, but less strongly correlated with total nitrogen or percent silt (Figure 3.6). Accordingly, both phosphorus and clay were higher in soils under forest compared to non-forest vegetation (Figure 3.6). However, there was considerable overlap of the ranges and quartiles of measured soil properties across vegetation types (Figure 3.6). Total phosphorus showed a systematic decrease across the forest - non-forest vegetation boundary (Figure 3.7).

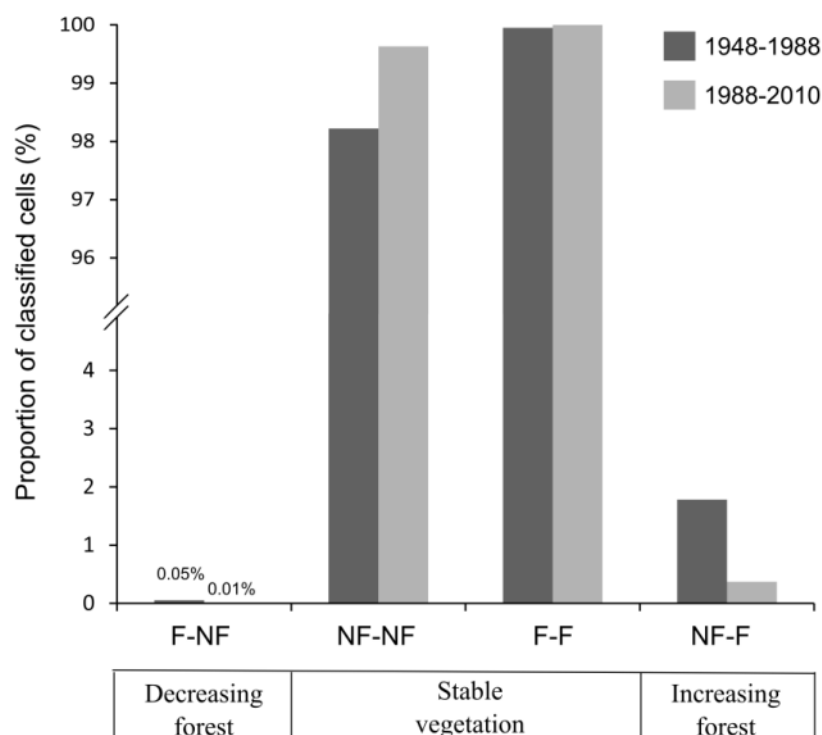


Figure 3.3. The proportion of cells ($n=58493$) from repeat aerial image analysis classified as forest (F) or non-forest (NF) that stayed the same (i.e. F-F or NF-NF) or changed (i.e. F-NF or NF-F) between 1948-1988 and 1988-2010 respectively. Indicative forest dynamics are indicated below the X axis. Note the break in the Y axis.

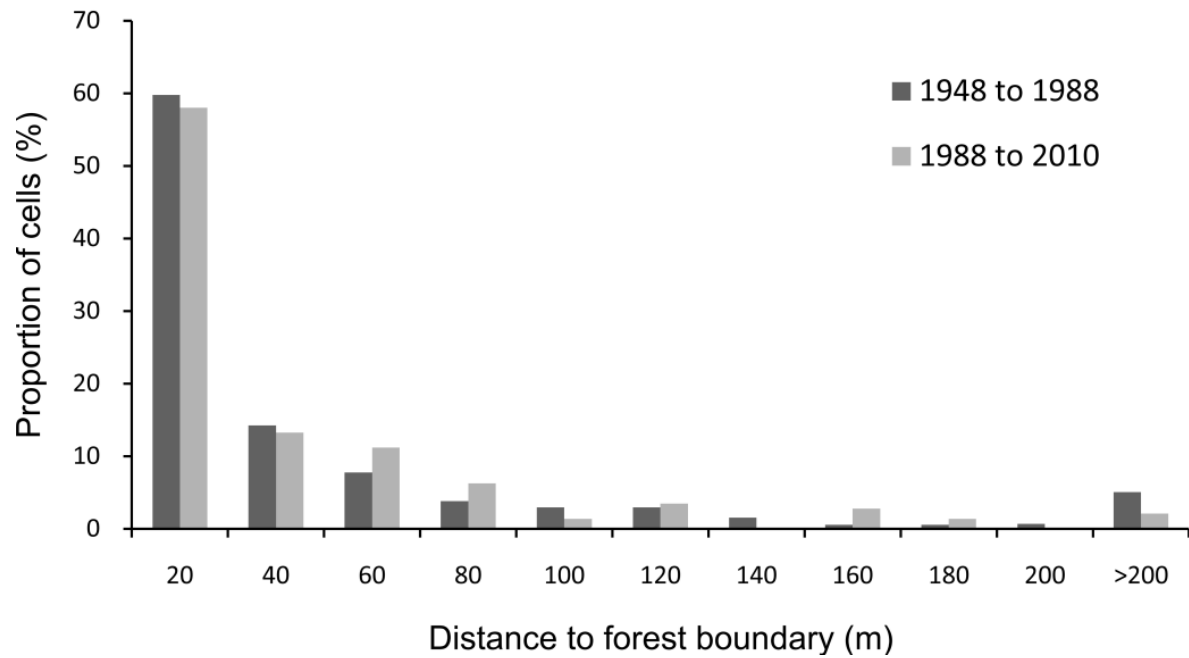


Figure 3.4. Proportion of all cells that transitioned from non-forest (NF) to forest (F) occurring at different distances from the forest boundary for the periods 1948-1988 and 1988-2010.

Topographic Variable	Non-forest to Forest (w_+)	
	1948 to 1988	1988 to 2010
Topographic position	0.99	0.25
Northness index	0.96	0.34
Elevation	0.31	0.30

Table 3.1. Importance values (Akaike weights, w_+) for topographic variables thought to explain the transition from non-forest to forest between 1948-1988 and 1988-2010 respectively.

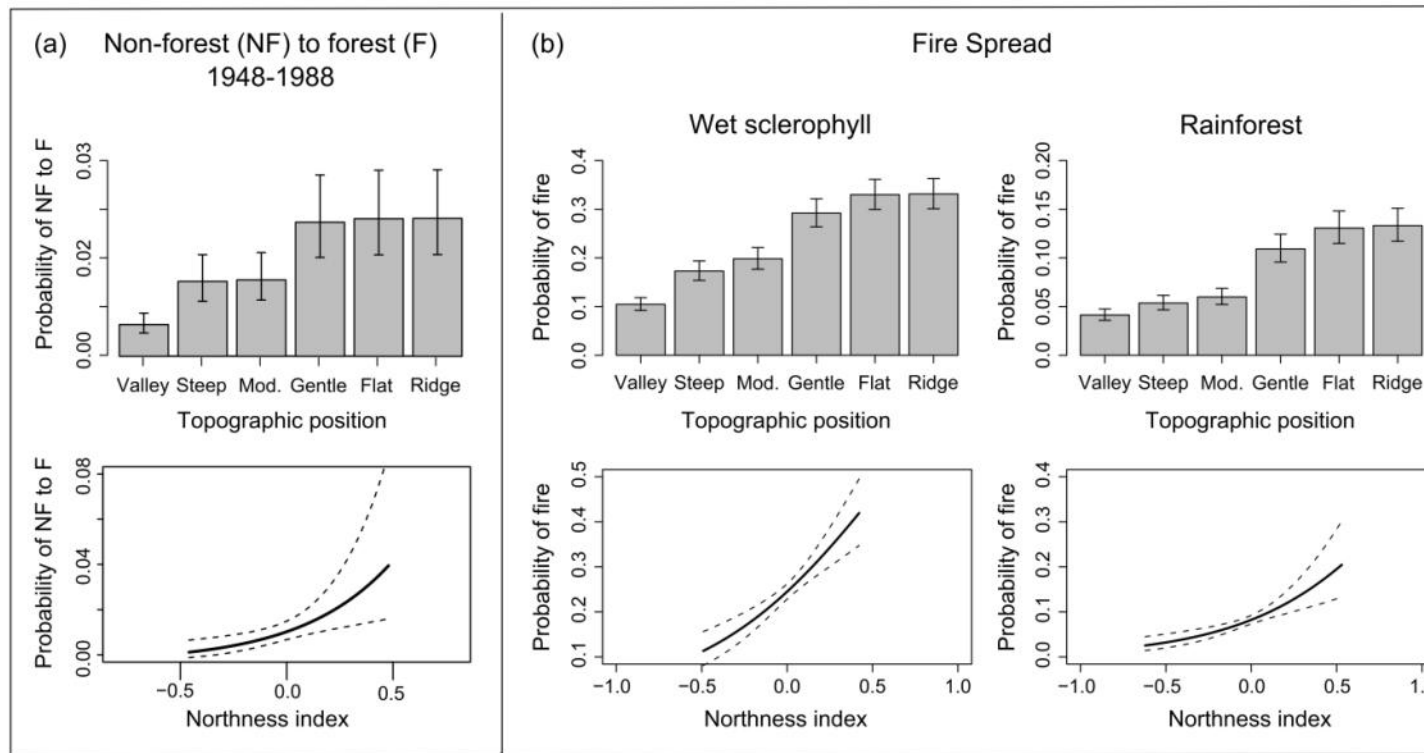


Figure 3.5. (a) shows the modelled relationship between parts of the landscape that changed from non-forest (NF) to forest (F) between 1948-1988 and topographic position and northness index. (b) shows the modelled relationship between fire occurrence and the same two topographic variables in wet sclerophyll and rainforest vegetation (see Wood *et al.*, 2011a, Figure 2.6). The northness index represents a gradient from steep southern slopes (strongly negative values) to steep northern slopes (strongly positive values). The 95% confidence intervals are shown.

		Forest		Non-Forest	
		Slope-Ridge	Valley-Flat	Slope-Ridge	Valley-Flat
Number of profiles		52	27	29	20
Organic horizon depth (cm)	mean	14.4	15.4	18.0	27.5
	range	(2.0-44.0)	(2.0-50.0)	(2.0-63.0)	(0.0-50.0)
Mineral horizon depth (cm)	mean	24.6	34.0	21.5	15.9
	range	(5.0-60.0)	(5.0-100.0)	(5.0-70.0)	(5.0-35.0)
Organic horizon texture (%)	Fibric	77	81	0	0
	Hemic	8	4	8	25
	Sapric	2	4	52	60
	Inorganic	13	11	10	15
Mineral horizon texture (%)	Sand	79.8	79.8	87.8	90.9
	Silt	15.8	17.3	11.9	9.0
	Clay	4.4	2.9	0.3	0.1

Table 3.2. Soil characteristics for soil profiles collected from two topographic settings ('run-off', slopes and ridges; 'run-on', valleys and flats) in forest and non-forest vegetation. The mode for organic horizon texture and mineral horizon texture are indicated in bold.

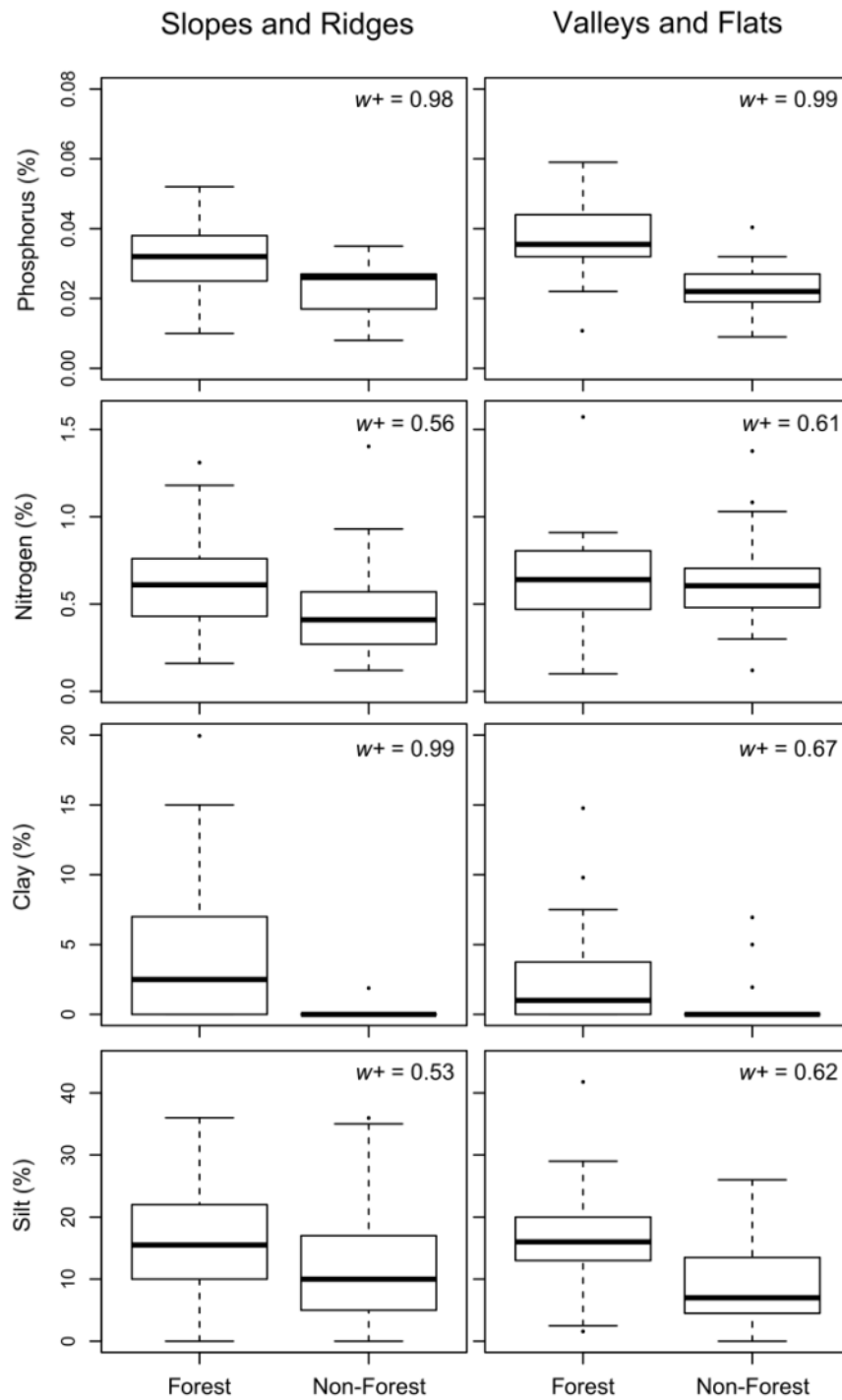


Figure 3.6. Box plots (median, quartiles, range) and importance values (Akaike weights, $w+$; inset) for four soil variables (phosphorus, nitrogen, clay, silt) thought to be correlated with the contrast between forest and non-forest vegetation in two topographic settings (‘run-off’ slopes and ridges; ‘run-on’ valleys and flats). Importance values were calculated separately for the two topographic settings.

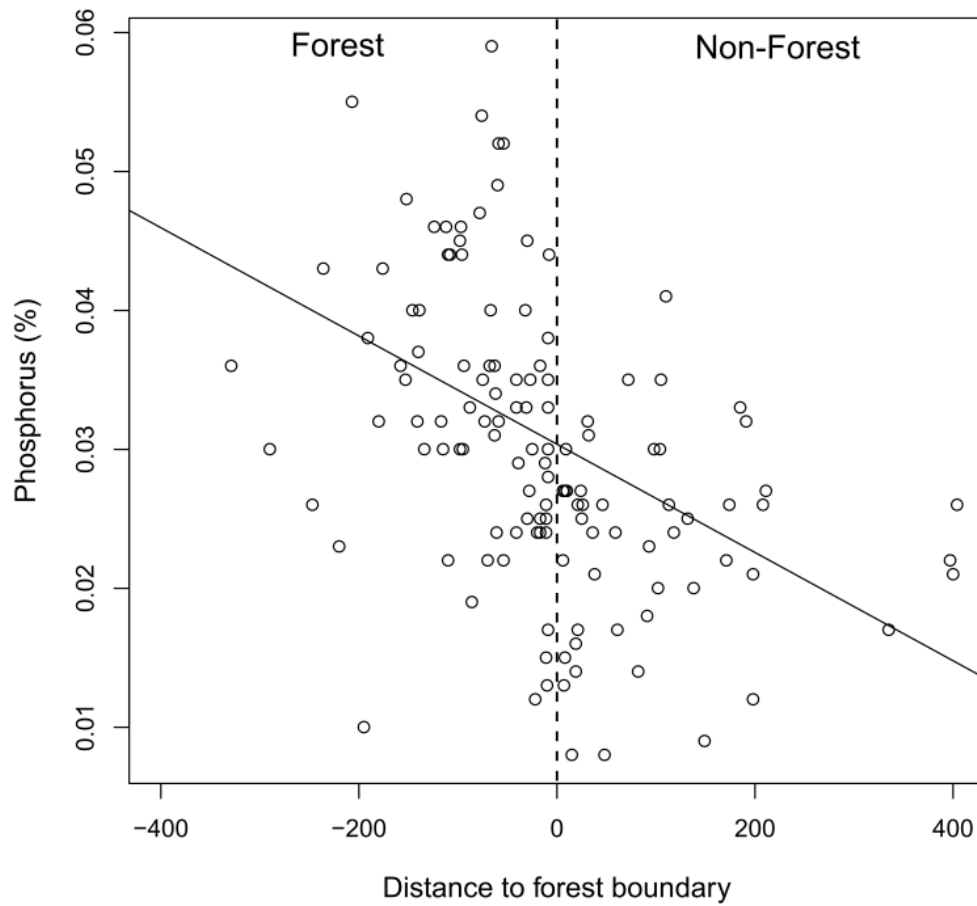


Figure 3.7. The trend in total phosphorus with distance from the forest – non-forest boundary. The dotted line indicates the position of the boundary. Negative distances refer to soil profiles within forest and positive distances refer to soil profiles within non-forest. A linear regression model was fitted to the data ($r^2 = 0.17$, $n = 128$).

Discussion

Vegetation dynamics from repeat image analysis

Our analysis of time-series aerial photography revealed remarkably stable vegetation patterns in the study area with the vast majority of classified vegetation remaining stable between 1948 and 2010 (62 years). Nevertheless, we identified some modest increases in forest cover. Between 1948 and 1988, forest cover in the study area increased by 4.1% and this increase was more likely to occur on forest edges associated with flats, ridges and steep northern slopes and less likely to occur in valleys and on steep southern slopes. These relationships between topographic positions and probability of forest cover change mirror the findings of Wood *et al.*, (2011a) who showed that forest fires in southwest Tasmania most commonly burn on ridges, flats and north facing slopes, and rarely burn in valleys and steep southern slopes (compare Figure 3.5a and Figure 3.5b). Collectively, this suggests that the increase in forest area prior to 1988 is linked to the regrowth and regeneration of trees following stand-replacing fire prior to 1948. Examination of available fire maps point to the 1933/34 fire that is estimated to have burnt approximately 22-24% of forest vegetation in southwest Tasmania (Marsden-Smedley, 1998; Marsden-Smedley and Kirkpatrick, 2000), however field studies within these areas of forest regeneration are required to rule out the possibility of currently unmapped pre-1948 fire events.

Between 1988 and 2010 forest cover increased by only 0.8% and this increase was not associated with topographic setting. There were few fires in the landscape in the two decades pre- or post- 1988 and this would explain why we found no support for a relationship between topographic settings conducive to fire and the increase in forest area. In the absence of post-fire recovery, we suggest that the forest increase during this period is due to the establishment of trees (largely by seed) in long unburnt moorland and low scrub

communities. It appears that this forest expansion was strongly associated with distance to forest edge and was extremely slow. Indeed, field evidence from long-term monitoring plots at Forest Lag within our study area (Figure 3.2) support our findings, with Brown *et al.*, (2002) reporting only minor shifts in the boundaries between moorland and scrub communities and no apparent shifts in the boundaries between scrub and forest over 20 years from 1980 to 2000.

The relatively low rate of forest expansion in our study area becomes apparent when compared with other studies that have analysed forest boundary dynamics using sequences of aerial photography in Australia. Discounting the 1948-1988 forest increase that we assume to be related to forest recovery following fire (see above), we estimate an increase of total forest cover of <1% over 62 years. In contrast, repeat aerial photography studies have revealed a 13-97% increase in monsoon rainforest cover in tropical savannas over 40-53 years in Northern Australia (reviewed by Bowman *et al.*, 2010), a 2%-8% increase in rainforest cover in a savanna matrix over 53 years in Far North Queensland (Tng *et al.*, 2010) and a 8%-12% increase in eucalypt and rainforest cover over 55 years in Northern Tasmania (Sanders, 2010). Given these emerging patterns of markedly different forest boundary dynamics observed across the Australian continent, it is likely that local factors (e.g. changed fire regimes, edaphic factors, land use history; Bowman, 2000) may be just as important as proposed continental factors (e.g. increased rainfall and/or CO₂ fertiliser effect; Bowman *et al.*, 2010) in driving landscape-scale vegetation dynamics.

The role of soil on vegetation stability

Our findings of higher phosphorus in forest compared to non-forest vegetation provide landscape scale confirmation of similar trends in phosphorus found across other boundaries in southwest Tasmania (Bowman *et al.*, 1986; Wood *et al.*, 2011b). This is consistent with

Jackson's (1968; 2000) hypothesis that repeat fires deplete nutrient stocks in the organic soils non-forest vegetation and that the absence of fire in forested vegetation allows net nutrient accumulation. Jackson (1968; 2000) and other studies proposing fire-mediated alternative stable states in vegetation (Wilson and Agnew, 1992; Perry and Enright, 2002; Hoffmann *et al.*, 2009; Murphy *et al.*, 2010; Odion *et al.*, 2010) argue that such gradients in soil nutrients engender an increased degree of resilience by contributing an additional barrier to tree growth (along with fire) in non-forest vegetation (i.e. Bond 2010) and facilitating rapid post-fire tree growth in forested vegetation (i.e. Hoffmann *et al.*, 2009).

Whether observed differences in phosphorus are the cause or the effect of vegetation and fire is difficult to untangle without manipulative experiments, although the trend of phosphorus decreasing (into non-forest) and increasing (into forest) systematically with distance from the forest boundary lends tentative support to the concept of fire-vegetation-soil feedbacks (Figure 3.7). Regardless of cause and effect, we posit that the observed phosphorus gradient would contribute to the extremely slow rate of forest expansion in our study area. Importantly, however, we do not suggest that phosphorus entirely precludes tree growth in non-forest areas given that forest vegetation was found to grow on soils with low levels of phosphorus (Figures 3.6 and 3.7; Wood *et al.*, 2011b). Other field studies show that western Tasmania rainforest vegetation grows on substrates with phosphorus concentrations only marginally higher than those found in moorlands in this study (Total phosphorus: 0.035%, 0.046% and 0.080% for Read 1995, Read 2001, Bowman *et al.*, 1986, respectively). Read (1995; 2001) also that soil phosphorus concentration did limit rainforest seedling growth. Reciprocal transplant experiments (i.e. Maranon and Bartolome, 1993; Peltzer, 2001), where forest species are planted in non-forest soil and vice versa, are an obvious pathway for future investigations into the influence of fire-vegetation-soil feedbacks in southwest Tasmania. The

effects of added nutrients and different burning regimes could be incorporated into these experiments.

Whilst there has been considerable attention focussed on the unique organic upper horizons of southwest Tasmanian soils (e.g. Bowman *et al.*, 1986; di Folco, 2007; Wood *et al.*, 2011b), the nature and characteristics of the underlying mineral horizons have been largely ignored (but see Balmer, 1990). We showed that the mineral soil horizons underlying all vegetation types in southwest Tasmania are dominated by sand – a result that is not surprising given the predominance of quartzitic substrates across the landscape. Our modelling showed that the clay content of mineral horizons constitute an important point of difference between soils associated with forest and non-forest vegetation on ridges and slopes, with percentage clay being higher in forest vegetation. However, despite the statistically significant trend we detected, the clay content of forested soils is still very low (Figure 3.6) and may not be functionally important to plant growth and therefore rates of forest expansion in southwest Tasmania. Therefore, we consider it unlikely that the underlying geological substrate and its mineral soils are controlling forest – non-forest boundaries associated with the Precambrian quartzites that dominate the Melaleuca Study Area and greater southwest Tasmania.

Alternative stable states in southwest Tasmania?

Whilst well documented theoretically, demonstrating alternative stable states in terrestrial landscapes with long lived species is inherently difficult, with few studies able to meet the criteria required to unambiguously demonstrate vegetation stability or persistence (Petraitis and Latham, 1999; Beisner *et al.*, 2003; Schroder *et al.*, 2005). Southwest Tasmania is no exception, however, the evidentiary basis upon which assessments of the proposed ecological models can be based (Table 3.3; see also reviews by Bowman, 2000; Bowman and Wood, 2009; Thomas *et al.*, 2010) is equivalent to most other studies that speculate fire-mediated

alternative stable states in similar terrestrial landscapes (e.g. Perry and Enright, 2002; Latham, 2003; Hoffman *et al.*, 2009; Warman and Moles, 2009; Odion *et al.*, 2010; Nicholas *et al.*, 2011).

The lowlands of southwest Tasmania have been the subject of a range of historical ecology studies that have revealed predominantly stable vegetation patterns at decadal to millennial time-scales (Table 3.3). This supports the concept of long term resilience of vegetation communities inferred by both Jackson (1968) and Mount (1979) (Figure 3.1). However, observations of localised vegetation transitions close to forest boundaries (Table 3.3) appear to be more congruent with the state-transition dynamics inherent in Jackson's (1968) alternative stable states model rather than the fixed vegetation boundaries postulated by Mount (1979). Nevertheless, our analyses of sequences of aerial photographs indicate that the expansion of forest into non-forest vegetation is far slower than Jackson (1968) implied.

The ubiquity of sand dominated mineral soil profiles with very low levels of clay across vegetation types in the Melaleuca Study Area indicate that the distribution and resilience of vegetation is not controlled by the geological substrate and its constituent mineral soils (i.e. Mount, 1979). Instead, it seems that a long history of human lit fires burning within a topographically complex landscape dictates the pattern of vegetation (Fletcher and Thomas, 2010a; Wood *et al.*, 2011a) and that the observed resilience of these vegetation patterns is related to a complex suite of stabilising feedbacks between fire and vegetation, and between fire, vegetation and soil (Table 3.3). Therefore, the available field evidence lends tentative support to the Jackson (1968) alternative stable states model as the most suitable model of vegetation dynamics in the lowlands of southwest Tasmania although significant modifications of the timeframes for transitions toward rainforest are required.

We caution that our conclusions are context specific and necessarily speculative for a number of reasons. Firstly, whilst we have shown that Jackson's (1968) model appears work well on Precambrian quartzites that dominate both the Melaleuca Study area and greater southwest Tasmania, the relationship between vegetation and geology in localised regions of southwest Tasmania with more complex geologies (i.e. where limestone, dolerite and quartzite intersect) remains untested. Secondly, the relationship between poorly drained, seasonally waterlogged valley flats and moorland vegetation (Pemberton, 1989) has not been investigated. These relationships underpin the Mount (1979) model and could be investigated using the spatial modelling framework of Wood *et al.*, (2011a) but significant improvements in spatial datasets are required before such modelling exercises can be undertaken.

That the vegetation communities of southwest Tasmania may represent a range of alternative stable states has important implications for the management of the regions high conservation value rainforest vegetation under projected climate and fire scenarios. It is clear from this study that transitions from non-forest to forest in southwest Tasmania are exceedingly slow and forest expansion may be further impeded by the drier, warmer summers and increased fire activity predicted for the region (Lucas *et al.*, 2007; Grose *et al.*, 2010). Under such conditions, rainforest vegetation relying on strong internal feedbacks for their maintenance become vulnerable to a so-called 'fire trap' (Hoffmann *et al.*, 2009; Odion *et al.*, 2010; Lindenmayer *et al.*, 2011). Feedbacks that maintain rainforest vegetation may be weakened by the drying out of currently wet and humid vegetation. Consequently, rapid transitions from rainforest to one of the more flammable communities become increasingly likely. These transitions are quickly reinforced by fire-vegetation-soil feedbacks, thus forcing a hysteresis in the system and creating a largely irreversible 'fire trap'. Detecting the onset of such transitions and subsequently restoring these landscapes presents a considerable management challenge (Hobbs and Suding, 2008).

Table 3.3: Field evidence from southwest Tasmania relating to key processes in the alternative stable states model of Jackson (1968) and the sharpening switch model of Mount (1979). Refer to Figure 3.1 for conceptual diagrams of the two models.

Hypothesis	Model	Evidence
Vegetation patterns largely resilient to change	Jackson and Mount	overall stability of core vegetation communities over 20 years based on permanent plots (Brown <i>et al.</i> , 2002) overall stability of core vegetation communities over 62 years based on aerial photography (this chapter) overall stability of vegetation communities throughout the Holocene inferred from pollen studies (Fletcher and Thomas, 2007, 2010a)
Transitions between vegetation types can occur	Jackson	vegetation transitions near forest boundaries over 20 years based on permanent plots (Brown <i>et al.</i> , 2002) and vegetation structure and floristics (Brown and Podger, 1982) vegetation transitions near forest boundaries over 62 years based on aerial photography (this chapter) rainforest converted to moorland by recurrent fires over ~100 years (Podger <i>et al.</i> , 1988)
Each vegetation community has a characteristic fire frequency (fire-vegetation feedback)	Jackson and Mount	time since fire varies systematically amongst vegetation communities (Jackson, 1968; Mount, 1979; Brown and Podger, 1982) flammability varies systematically amongst vegetation communities (Marsden-Smedley and Kirkpatrick, 2000; Wood <i>et al.</i> , 2011a) rainforest communities limited to infrequently burnt topographic fire refugia (Wood <i>et al.</i> , 2011a) and fire-protected islands (Wood <i>et al.</i> , 2011b)
Each vegetation community has a characteristic soil nutrient status (fire-vegetation-soil feedback)	Jackson	nutrient status of organic soils varies systematically according to vegetation and putative fire frequency (Bowman <i>et al.</i> , 1986; Jackson, 2000; Wood <i>et al.</i> , 2011b, this chapter)
Vegetation distribution dictated by physical environmental variables (i.e. site factors)	Mount	no functionally relevant gradient in mineral soil across vegetation boundaries in landscapes dominated by Precambrian quartzites (Balmer, 1990, this chapter) not tested for drainage patterns and geologically complex landscapes.

Chapter 4: Fire-patterned vegetation and the development of organic soils in the lowland vegetation mosaics of southwest Tasmania

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Abstract

Two contrasting ecological models have been proposed for the forest – moorland vegetation mosaics of southwest Tasmania that stress different interactions between fire, soils, vegetation and the physical environment to produce either stable or dynamic vegetation patterns. We investigated aspects of these models by sampling organic soil profiles across vegetation mosaics to determine variation in soil depth, organic carbon content, nutrient capital, stable carbon isotope composition ($\delta^{13}\text{C}$) and ^{14}C radiocarbon age in two contrasting landscape settings. ^{14}C basal ages of organic soils ranged from recent (< 400 calibrated yrs BP) to mid Holocene (~ 7200 cal. yrs BP), with a tendency for older soils to be from poorly drained moorlands and younger soils from the forest. The long-term net rate of carbon accumulation ranged from 2.7 to $19.2 \text{ gC m}^{-2} \text{ yr}^{-1}$, which is low compared to Northern Hemisphere peatland systems. We found that $\delta^{13}\text{C}$ in organic soil profiles cannot be used to infer Holocene vegetation boundary dynamics in these systems. We found a systematic decrease of phosphorus from rainforest through eucalypt to moorland, but estimated that phosphorus capital in moorland soils was still sufficient for the development of forest vegetation. Our results suggest that the characteristics of organic soils across the landscape are the result of interactions between not only vegetation and fire frequency, but also other factors such as drainage and topography.

Introduction

One of the earliest examples of fire-mediated alternative stable states (Petraitis and Latham, 1999; Warman and Moles, 2009; Odion *et al.*, 2010) in the literature was put forward by Jackson (1968) for the mosaic of treeless moorland, sclerophyll forest and rainforest that occupy the rugged landscapes of southwest Tasmania. Indeed, the ecological ideas inherent

within the ‘ecological drift’ model of Jackson (1968) have been at the forefront of many avenues of fire ecology research (reviewed by Bowman and Wood, 2009). Jackson (1968) argued that southwest Tasmania has an ideal climate for temperate rainforest and that there is no aspect, soil type or edaphic situation that could not support rainforest. He attributed the presence of vast tracts of moorland and sclerophyll forest to a long history of landscape scale fires and implicitly included humans as a primary ignition source for these fires (Jackson, 1999). The resulting ‘cultural landscape’ (*sensu* Fletcher and Thomas, 2010a) of southwest Tasmania is of significant conservation value and forms a large part of the Tasmanian Wilderness World Heritage Area.

The ecological model proposed by Jackson (1968) is based on a series of positive feedback ‘switches’ (*sensu* Wilson and Agnew, 1992) between vegetation, fire frequency and soil fertility that result in an inherent resilience to change and the maintenance of alternate vegetation communities over time (see also Bowman and Jackson, 1981). Accordingly, the characteristic frequency of fire in each vegetation community declines from highly flammable moorlands, through sclerophyll scrub and forest, to non-flammable rainforest. Importantly, Jackson (1968) also included the possibility that chance deviations in fire frequencies – assumed to be highly improbable – can cause a shift to another vegetation community. This is consistent with state-transition dynamics predicted by alternative stable state theory (Scheffer *et al.*, 2001; Scheffer and Carpenter, 2003). Jackson (1968, 2000) also argued that fire frequency and the fertility of the ubiquitous organic soils of the region (di Folco, 2007) interact in an inverse fashion due to the destruction of soil layers (e.g. Pemberton, 1988), the volatilisation of key elements (e.g. Harwood and Jackson, 1975) and post-fire losses due to run-off and leaching (Bowman and Jackson, 1981). To date, published studies on the nutrient status of soils in southwest Tasmania that explicitly test these interactions across vegetation types (reviewed by Jackson, 2000) are limited to a single

transect from moorland through eucalypt forest to rainforest by Bowman *et al.* (1986), which offered broad support to Jackson's (1968) model.

Whilst Jackson (1968) allowed for dynamic vegetation community transitions, an alternative model proposed by Mount (1979) argued that the positive feedbacks between fire frequency and vegetation were strong enough to eliminate the chance of vegetation state transitions, resulting in stable vegetation communities in southwest Tasmania. Mount (1979) suggested that this stability was due to the overriding influence of physical environmental factors such as geology, topography and drainage on vegetation communities and their characteristic fire frequencies. Field studies (Balmer, 1990; Brown and Podger, 1982a; Bowman *et al.*, 1986; Brown *et al.*, 2002), modelling approaches (Henderson and Wilkins, 1975; King *et al.*, 2006) and palynological studies (Macphail, 1979; Markgraf *et al.*, 1986; Colhoun, 1996) have fostered a broad acceptance of the dynamic Jackson model of vegetation dynamics for southwest Tasmania (Jackson and Brown, 1999; Bowman, 2000; Brown *et al.*, 2002; Bowman and Wood, 2009). However, more recent reconstructions of post-glacial vegetation trends have revealed a remarkable degree of stability in the distribution of vegetation types throughout the Holocene (Fletcher and Thomas, 2007a; 2010a,b), thus provoking renewed interest in Mount's (1979) stable fire cycles model (Macphail, 2010; Thomas *et al.* 2010).

Evidence of changes in ratio of ^{13}C and ^{12}C stable carbon isotopes ($\delta^{13}\text{C}$) in soil organic matter down soil profiles has been used to detect the degree of stability of vegetation communities over time (Witt, 2002). The application of $\delta^{13}\text{C}$ analyses to studies of vegetation change is based on the assumption that isotopic composition (i.e. $\delta^{13}\text{C}$) of soil organic matter and vegetation are similar, and that shifts in the isotopic composition of the vegetation over time are recorded in the soil (Witt, 2002). This method is particularly useful in grassland - forest ecosystems where grasses with the C4 photosynthetic pathway have a distinct $\delta^{13}\text{C}$

signature (-17 to -9‰) compared with that of woody plants with the C3 photosynthetic pathway (-32 to -22‰). When combined with ^{14}C radiocarbon dating, this method has been used to reconstruct vegetation transitions for a range of grassland - forest landscapes (Schwartz *et al.*, 1996; Boutton *et al.*, 1998; Bowman and Cook, 2002; Bowman *et al.*, 2004; Krull and Bray, 2005; Krull *et al.*, 2007). Although all species in southwest Tasmania use the C3 photosynthetic pathway, it is possible that variation in $\delta^{13}\text{C}$ values within C3 plants (Heaton, 1999; Dawson *et al.*, 2002) may result in distinct $\delta^{13}\text{C}$ signatures for low open moorland vegetation and tall closed forest vegetation communities, hence facilitating the detection of vegetation transitions (i.e. Jackson, 1968) or vegetation stability (i.e. Mount, 1979) from $\delta^{13}\text{C}$ signatures in soil organic matter.

The extent to which the nutrient-poor soils of southwest Tasmanian moorlands limit the development of forest vegetation is an important aspect of the proposed ecological models. Jackson (1968) argued that frequent fires in moorlands deplete nutrient stocks to an extent that impedes the development of forest vegetation, thus creating a positive feedback between fire, vegetation and soils (i.e. a two factor switch, Wilson and Agnew, 1992). In a recent review, Bond (2010) assembled data on nutrient pools in foliage, woody biomass and soil for a range of forests, savannahs and grasslands to calculate the nutrient stocks required for constructing the woody biomass needed of forest vegetation. Bond (2010) applied these threshold values as a 'rule of thumb' to identify whether particular open treeless environments have sufficient soil nutrient capital to support woody vegetation. This approach appears particularly useful for examining similar questions in the moorlands of southwest Tasmania.

The primary objective of this study was to test the applicability of using $\delta^{13}\text{C}$ and ^{14}C radiocarbon dating in organic soils for investigating the temporal dynamics of forest –

moorland boundaries in southwest Tasmania. We sampled the organic component of soil profiles from moorland, sclerophyll scrub, eucalypt forest and rainforest in two contrasting landscape settings (estuarine and riverine) to determine (a) the age of the basal and mid layers of soil profiles using accelerator mass spectrometry (AMS) radiocarbon dating; and (b) $\delta^{13}\text{C}$ signatures of the overlying vegetation, surface litter, and the upper, mid and basal sections of each of these soil profiles. Our data on the basal age and organic carbon content of these soil profiles also allow us to calculate the long-term net rate of carbon accumulation (LORCA: Clymo, 1984). The organic soils of southwest Tasmania are likely to constitute a significant store of below ground carbon (di Folco, 2007). LORCA is commonly used to characterise the temporal dynamics of carbon in peatland ecosystems (e.g. Korhola *et al.*, 1995; Borren *et al.*, 2004) but published estimates are lacking for Tasmanian or Australian organic soils. Therefore, we present preliminary estimates of LORCA for Tasmanian organic soils, discuss their limitations and contextualise these estimates by comparison with estimates of LORCA from peatland ecosystems in the Northern Hemisphere.

Our secondary objective was to measure the physical (depth, bulk density) and chemical characteristics (carbon, cation exchange capacity, nitrogen and phosphorus) of organic soils in these two landscape settings, and to combine this information with ^{14}C age data, to provide insights into the relationships between fire, vegetation, the physical environment and soil development. This data also allowed us to evaluate whether the nutrient capital of moorland soils was higher or lower than the amount required to ‘build’ forest vegetation as calculated by Bond (2010). The sampling design (i.e. eight soil profiles from two transects, see below) for this aspect of our study was constrained by the cost of ^{14}C radiocarbon dating and the remote location of our study sites. Indeed, most palaeoecological (reviewed by Thomas *et al.*, 2010) and ecological field studies into vegetation (e.g. Brown and Podger, 1982a; Balmer, 1990; Brown *et al.*, 2002) and soils (e.g. Bowman *et al.*, 1986) for this wilderness region are

limited in geographic extent and/or replication. Thus we present results on the physical and chemical characteristics of organic soils to contribute to the scant published soil nutrient data, and, whilst acknowledging the limitations of our dataset, discuss the implications for our understanding of organic soil development and the ecological models of Jackson (1968) and Mount (1979).

Methods

Landscape setting and transects

Two vegetation mosaics were sampled in contrasting landscape settings using transects that intersected the dominant vegetation types. One site was at an estuarine setting at Forest Lag on Bathurst Harbour and the other was at a riverine setting on the Louisa River Plains (Figure 4.1). The landscape at Forest Lag has a complex topography associated with a drowned valley underlain by comparatively unmetamorphosed Precambrian conglomerates in a sandstone-mudstone matrix (Williams and Corbett, 1977). The site has been the focus of several studies into the relationships between fire regimes and the floristics of southwest Tasmanian vegetation communities (Brown and Podger, 1982a; Brown *et al.*, 2002). The Louisa Plains landscape is characterised by broad terraced plains derived from redeposited outwash material from multiple glaciations during the Quaternary (Macphail *et al.*, 1999). These plains have been more recently overlaid by alluvial sediments and shallow to deep organic soils. The plains are dominated by moorland vegetation, with sclerophyll communities and rainforest occurring along the Louisa River. The Louisa Plains are renowned for the presence of small, circular ‘peat mounds’ (<30 m diameter) which rise several meters above the plains and are often colonised by scrub and sclerophyll communities (Macphail *et al.*, 1999).

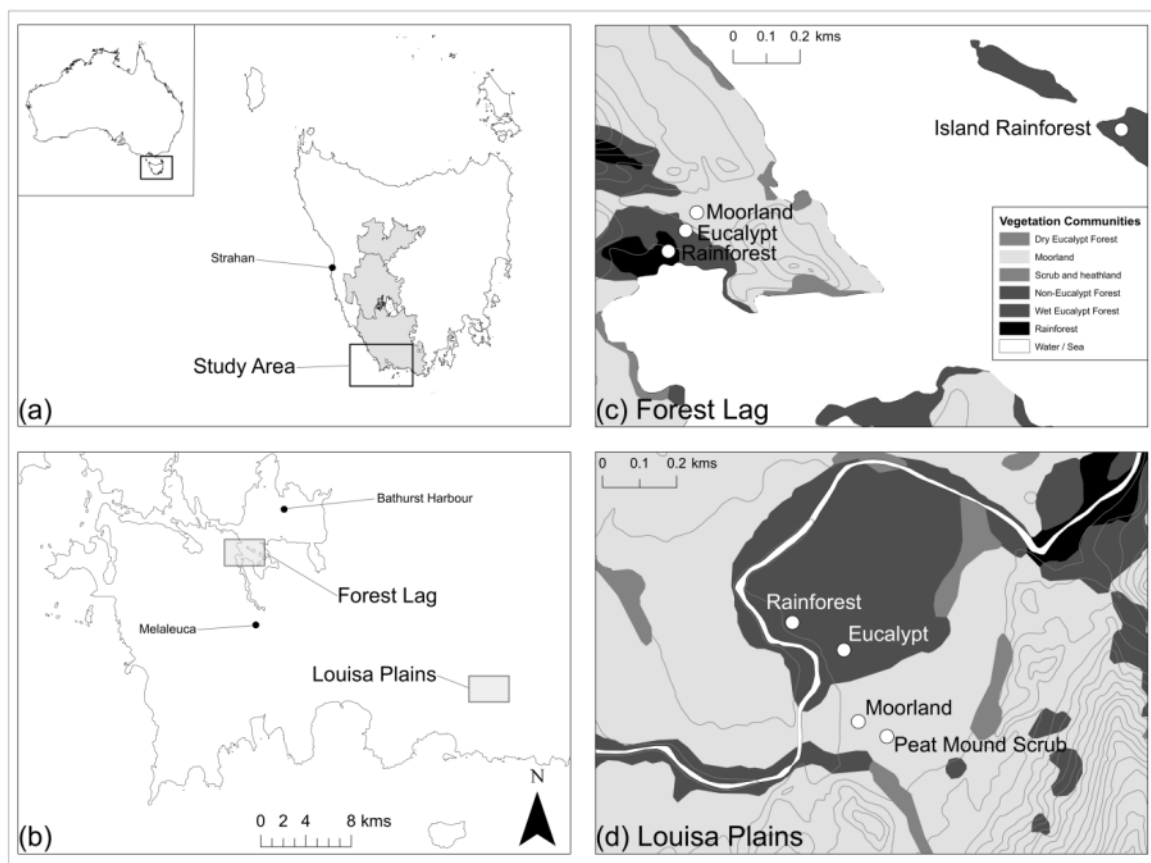


Figure 4.1. Map showing the location of (a) Tasmania, the Tasmanian Wilderness World Heritage Area (shaded) and the Study Area (box); (b) the Forest Lag and Louisa Plains landscape settings; (c) vegetation communities and soil profiles at Forest Lag; (d) vegetation communities and soil profiles at Louisa Plains. Other sites mentioned in the text are indicated. Vegetation community classifications are from the Tasmanian Vegetation Mapping Program (TASVEG: Harris and Kitchener, 2005).

We sampled from four soil pits at Forest Lag and four soil pits at Louisa Plains (Figure 4.1; Figure 4.2). At each location we established a single transect that encompassed the full range of vegetation communities and dug a soil pit at the beginning (rainforest), middle (eucalypt) and end (moorland) of these transects. The dominant species found in each vegetation type are listed in Table 4.1. At Forest Lag, a fourth profile was established within a rainforest on the nearby (~1 km) Celery Top Islands: a prime example of long-unburnt vegetation on relatively flat terrain in a landscape setting that is highly protected from fire. At Louisa

Plains, a fourth profile was sampled in low sclerophyll scrub vegetation that had colonised a peat mound directly adjacent to the moorland profile. The Forest Lag transect straddled a ridge and was originally established by Brown and Podger (1982a). The boundary of the vegetation communities for both transects appeared to be related to topographic protection from fire, with the forest-moorland boundary at Forest Lag following the top of a ridgeline and the forest - moorland boundary at Louisa Plains following a small tributary (and an associated terrace) that dissected the floodplain.

Soil sampling and analysis

Samples were collected every 10 cm from the surface to the base of the organic soil profile for each of the eight profiles. The degree of humification down the profile was classified using a simplified von Post scale as fibric, hemic or sapric (Isbell, 2002). Two samples were collected from each 10 cm layer. The first sample provided material for physical and chemical analyses, and for $\delta^{13}\text{C}$ and AMS ^{14}C determinations. The second sample was collected with a 6 cm diameter sampling ring of known volume and later used for the measurement of bulk density. All soil samples were stored in sealed plastic bags and returned to the laboratory where they were air dried, weighed and sieved to remove the gravel fraction (>2 mm). Air dry bulk density was calculated using the bulk density ring samples and later corrected to oven dry bulk density using the moisture content of a 5 g subsample oven dried at 105 °C for 48 hours. The organic content of each sample was derived by loss on ignition, where 5-10 g samples were combusted at 550 °C for 6 hours. Percent soil organic carbon (%C) was calculated from loss on ignition (LOI) according to the methods outlined by Isbell (2002), assuming that the mineral fraction has no clay (i.e. %C = LOI x 0.5). The depth of the organic soil horizon was defined according to the Australian Soil Classification (Isbell, 2002) definition of an organosol (i.e. 12 % or more organic carbon). For determination of total

Kjeldahl nitrogen, samples were digested at 360 °C with sulphuric acid and copper sulphate catalyst. The digest was then analysed using flow injection analysis (Lachat QuikChem 8000; Loveland CO, USA; Lachat method 13-107-06-2-D). Soluble, inorganic nitrate was extracted from the soil samples by shaking 5 g of soil for 30 minutes at room temperature with 50mL of 2M KCl solution. The nitrate was reduced quantitatively by cadmium to nitrite and determined by a colorimetric method using flow injection analysis (Lachat QuikChem 8000, Loveland CO, USA; Lachat method 12-107-04-1-B). For determination of total Kjeldahl phosphorus, samples were digested at 360 °C with sulphuric acid and copper sulphate catalyst. The digest was then analysed using flow injection analysis (Lachat QuikChem 8000; Loveland CO, USA; Lachat method 10-115-01-1-D). Effective Cation Exchange Capacity was determined using Rayment and Higginson (1992) method 15J1.

For each profile, soil samples representing the upper, mid and basal sections of each profile were selected to investigate $\delta^{13}\text{C}$ composition down the profile and for ^{14}C AMS radiocarbon dating. These samples were wet sieved and particles from the 53-250 μm size fraction were recovered. The samples contained high levels of humic acids (Colhoun, 1986). Therefore, before ^{14}C AMS dating and ^{13}C stable isotope analyses each sample underwent thorough acid-alkaline-acid pre-treatment (Hua *et al.*, 2001) with particular emphasis on chemical treatment with alkaline solution. Pre-treated samples from the mid and basal samples were converted to CO_2 then graphite (Hua *et al.*, 2001) for AMS ^{14}C measurement using the STAR facility at ANSTO (Fink *et al.*, 2004). The first and last acid treatments used 2M HCl at 60°C for 2 hrs and at room temperature for 14 hrs, respectively. The alkaline step employed NaOH solution of 0.5-2% at 60°C for 7-22 hrs depending on the level of humic acid. Stable carbon isotope ratios were determined for each sample following the methods described in Bowman and Cook (2002) and were expressed relative to the Vienna-PDB standard (Peterson and Fry, 1987).

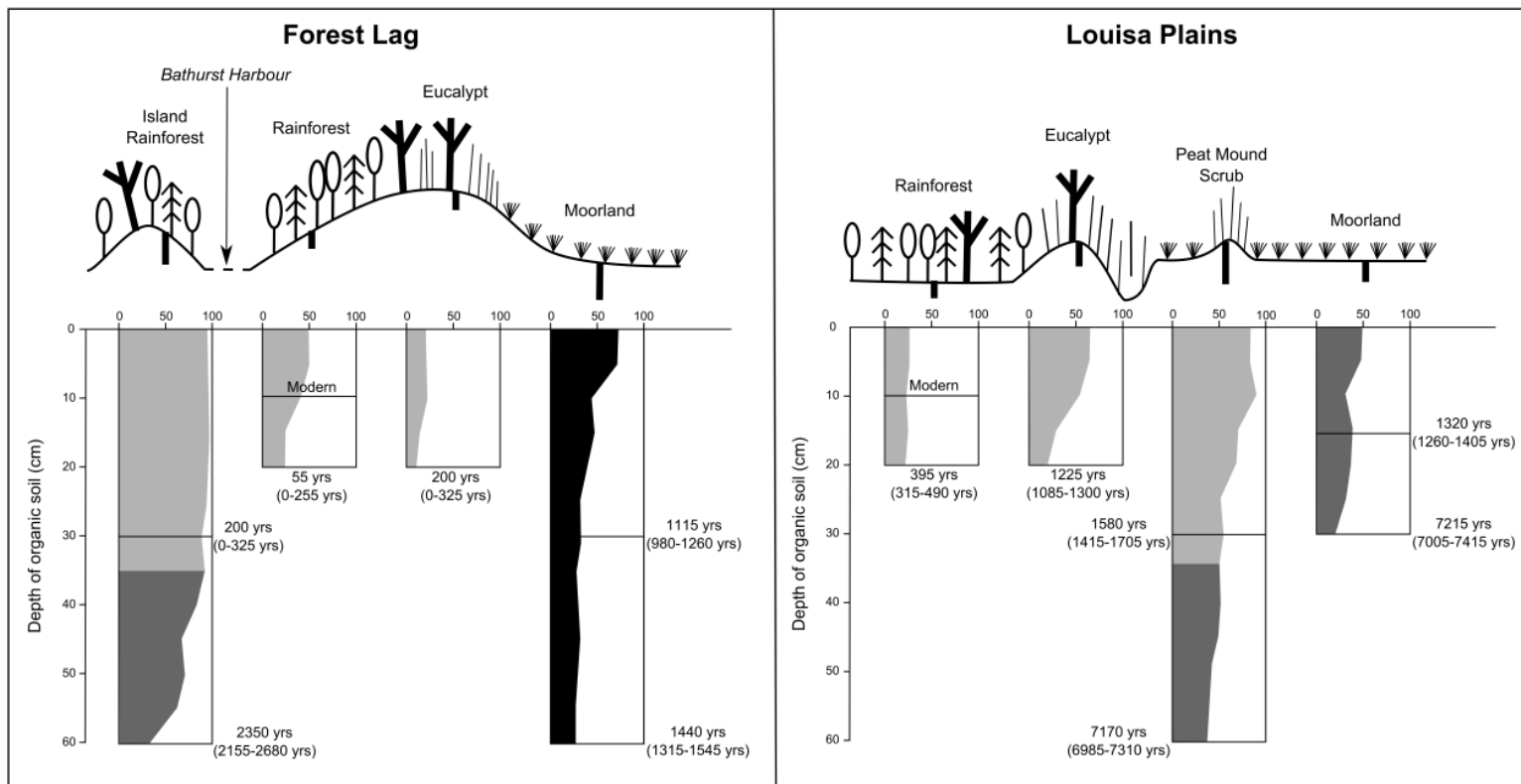


Figure 4.2. The depth (y axis), percent organic matter (x axis) and mid and basal calibrated ^{14}C age (median cal. yrs BP and 2σ age range shown) of the organic soil profiles at the Forest Lag and Louisa Plains landscape settings. The local terrain and vegetation structure is illustrated for each profile. The degree of humification of organic matter is shaded as follows: sapric (black), hemic (dark grey) and fibric (light grey). Details of mid and basal calibrated ^{14}C ages are given in Table 4.2.

Foliage samples of the dominant species of each vegetation community, and hand samples of the heavily decomposed surface layer around each soil profile were collected and stored in sealable plastic bags. These were dried and finely ground in the laboratory and the stable carbon isotope ratios were determined following the methods described in Bowman and Cook (2002). Species were categorised into the communities, rainforest, eucalyptus scrub and moorland according to Brown and Podger (1982a).

Data analysis and calculations

The mass of carbon, nitrogen and phosphorus, in g m^{-2} , was calculated for each 10 cm soil layer from bulk density measurements and carbon and nutrient concentrations. This data was used to (a) investigate the relationship between the mass of soil organic carbon and the mass of soil nutrients using Pearson correlation coefficients, and (b) calculate the carbon and nutrient capital in the upper 20 cm (common to all profiles) and to the full depth of each profile. To explore similarities amongst profiles we used non metric multidimensional scaling (NMDS) in the vegan package in R.2.10.1 (Oksanen *et al.*, 2010). The ordination was based on variables attributable to the soil profiles, namely: soil depth, calibrated ^{14}C basal age, mass of carbon, nitrogen and phosphorus, bulk density and cation exchange capacity and the degree of humification. All the variables were standardised to a 0 - 1 scale. The vertical accretion rate, in mm yr^{-1} , was calculated by dividing the total depth by the calibrated ^{14}C basal age. The long-term net rate of carbon accumulation (LORCA: $\text{g m}^{-2} \text{yr}^{-1}$) was calculated by dividing the total amount of accumulated carbon per unit area by the median calibrated ^{14}C basal age (Clymo, 1984; Borren *et al.*, 2004). These calculated rates assume that organic matter accumulation has been linear (see discussion); that no recycling of carbon has taken place; and that the carbon fraction as analysed has not moved up or down the profile.

Species	$\delta^{13}\text{C}$ (‰)
Rainforest	
<i>Phyllocladus aspleniifolius</i>	-28.9
<i>Anopterus glandulosus</i>	-30.9
<i>Cenarrhenes nitida</i>	-32.5
<i>Eucryphia lucida</i>	-31.5
<i>Nothofagus cunninhamii</i>	-31.0
<i>Anodopetalum biglandulosum</i>	-29.8
Eucalypt Scrub	
<i>Gahnia grandis</i>	-30.5 (\pm 0.6)
<i>Banksia marginata</i>	-31.1
<i>Leptospermum glaucescens</i>	-30.5 (\pm 0.6)
<i>Nematolepis squamea</i>	-31.3
<i>Acacia verticillata</i>	-32.2
<i>Eucalyptus nitida</i>	-31.1
<i>Monotoca glauca</i>	-31.3
<i>Cyathodes juniperina</i>	-31.4
Moorland	
<i>Leptospermum nitidum</i>	-28.6
<i>Agastachys odorata</i>	-28.8
<i>Melaleuca squarrosa</i>	-28.2
<i>Melaleuca squamea</i>	-29.4 (\pm 0.6)
<i>Bauera rubioides</i>	-29.1
<i>Boronia citriodora</i>	-29.6
<i>Gymnoschoenus sphaerocephalus</i>	-25.7
<i>Sprengelia incarnata</i>	-30.1
<i>Baekea leptocaulis</i>	-28.7
<i>Leptocarpus tenax</i>	-27.2
<i>Leucopogon parviflorus</i>	-28.4 (\pm 0.6)

Table 4.1. $\delta^{13}\text{C}$ (‰) values for a plant species found in rainforest, eucalypt scrub and moorland in southwest Tasmania. Plant species were assigned communities according to Brown and Podger (1982a). Unless otherwise stated, the standard deviation of the repeat sample measurements was less than or equal to \pm 0.4‰.

Results

Physical characteristics and age of organic soil profiles

The two dimensional NMDS ordination strongly segregated the soil profiles (Figure 4.3). On the extremes of the first axis the rainforest and eucalypt forest profiles were strongly separated from the moorland profiles and the Celery Top Island rainforest profile. The two mainland rainforest profiles were shown to be highly similar to each other. On the second axis there was a gradient from the moorland profiles through the Louisa Plains scrub peat mound to the rainforest profile on Celery Top Island (Figure 4.3).

The two mainland rainforest profiles and the two eucalypt forest profiles were shallow ($\leq 20\text{cm}$), fibric, and low in organic matter (Figure 4.2). The median calibrated ^{14}C basal dates (Figure 4.2; Table 4.2) for these four forested profiles ranged from 55 cal. yrs BP (2σ range: 0-255 cal. yrs BP) to 1225 cal. yrs BP (2σ range: 1085-1300 cal. yrs BP). In contrast, the moorland profiles, the Louisa Plains scrub peat mound and the Celery Top Island rainforest profile were deeper and comprised a higher percentage of organic matter with a higher degree of humification (Figure 4.2). The median calibrated ^{14}C basal dates (Figure 4.2; Table 4.2) for these four profiles ranged from 1440 cal. yrs BP (2σ range: 1315-1545 cal. yrs BP) to 7215 cal. yrs BP (2σ range: 7005-7415 cal. yrs BP).

	Conventional				Calibrated ¹⁴ C age		Lab #
	Section	Depth (cm)	¹⁴ C age		(cal. yrs BP)†		
			yrs BP	1σ	Med. Prob.	2σ age range	
Forest Lag							
CT Rainf.	Mid	30	240	45	200	0-325	OZK849
CT Rainf.	Basal	60	2385	50	2350	2155-2680	OZK850
Rainforest	Mid	10	Modern‡		Modern‡		OZK847
Rainforest	Basal	20	60	35	55	0-255	OZK848
Eucalypt	Basal	20	240	45	200	0-325	OZK851
Moorland	Mid	30	1245	45	1115	980-1260	OZK852
Moorland	Basal	60	1600	60	1440	1315-1545	OZK853
Louisa Plains							
Rainforest	Mid	10	Modern‡		Modern‡		OZK855
Rainforest	Basal	20	375	40	395	315-490	OZK856
Eucalypt	Basal	20	1350	50	1225	1085-1300	OZK859
PM Scrub	Mid	30	1730	50	1580	1415-1705	OZK857
PM Scrub	Basal	60	6310	60	7170	6985-7310	OZK858
Moorland	Mid	15	1460	50	1320	1260-1405	OZK860
Moorland	Basal	30	6340	60	7215	7005-7415	OZK861

[‡] - Modern is post 1950 AD

[†] - Radiocarbon calibration was performed using Southern Hemisphere data set SHCal04 (McCormac *et al.*, 2004) and calibration program CALIB 5.0.1 (Stuiver *et al.*, 2005)

Table 4.2. Conventional and calibrated ^{14}C ages for the mid and basal sections of each organic soil profile at Forest Lag and Louisa Plains. Mid profile ^{14}C ages were not obtained for the eucalypt profiles. CT Rainf. is Celery Top Island Rainforest. PM Scrub is Peat Mount Scrub.

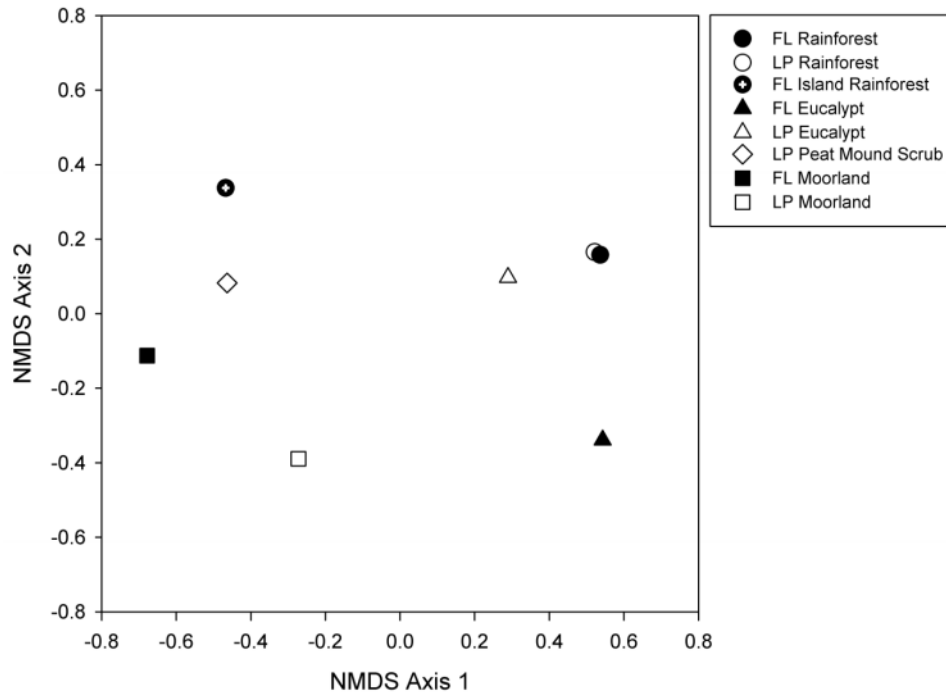


Figure 4.3. Plot showing ordination points from the first and second dimensions of the non metric multidimensional scaling (NMDS) of soil profile variables: soil depth, ^{14}C basal age, mass of carbon, nitrogen and phosphorus, bulk density and cation exchange capacity and the degree of humification. Solid symbols are for Forest Lag (FL) and hollow symbols are for Louisa Plains (LP). The stress level of the NMDS was 0.67.

$\delta^{13}\text{C}$ of vegetation and organic soil

$\delta^{13}\text{C}$ values of vegetative samples from plant species from rainforest, eucalypt scrub and moorland ranged from -25.7‰ to -32.5‰ (Table 4.1). Mean $\delta^{13}\text{C}$ values for species associated with each vegetation community indicate that moorland species were significantly more ^{13}C enriched (one-way ANOVA, $P < 0.05$) than species associated with rainforest and eucalypt scrub, albeit by only 2.3‰ to 2.7‰ respectively (Figure 4.4). The magnitude of the difference between $\delta^{13}\text{C}$ values of the partially decomposed surface litter sampled within each vegetation community was small ($< 1\%$) and $\delta^{13}\text{C}$ values in soil organic matter at different levels down the profile were relatively constant and showed little variation across the vegetation communities (Figure 4.5).

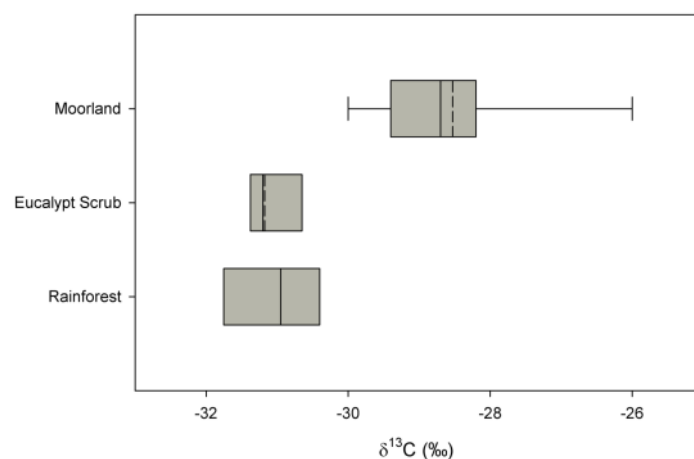


Figure 4.4. Boxplot of $\delta^{13}\text{C}$ (‰) values for plant samples from: rainforest (n=6), eucalypt scrub (n=8) and moorland (n=11). The box includes the mean (dashed line), median (solid line) and the 25th and 75th percentiles. Error bars indicate the 10th and 90th percentiles. There was insufficient data to calculate error bars for rainforest and eucalypt scrub. Species groupings into vegetation communities are shown in Table 4.1.

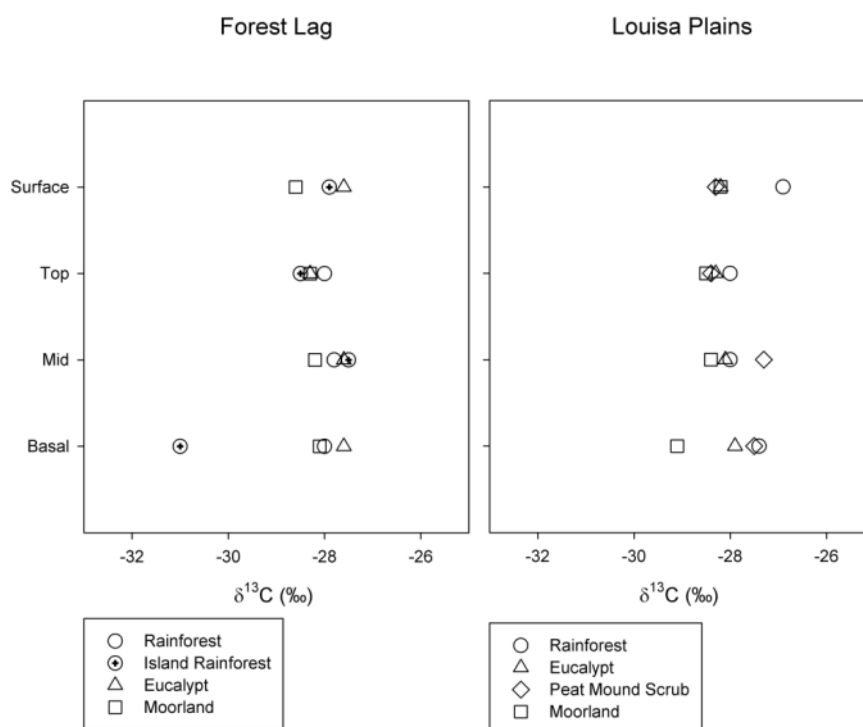


Figure 4.5. $\delta^{13}\text{C}$ (‰) values of partially decomposed surface litter and soil organic matter from the upper, mid and basal sections of each soil profile at Forest Lag and Louisa Plains.

Long term net rate of carbon accumulation (LORCA)

The shallow rainforest and eucalypt profiles had relatively recent ^{14}C basal dates (55 – 1225 median cal. yrs BP; Table 4.2) and seem to have a higher turnover of soil organic matter compared to the deeper moorland, scrub and Celery Top Island rainforest profiles which have been accumulating organic matter for thousands of years (1440 – 7215 median cal. yrs BP; Table 4.2). These two sets of four profiles are clearly separated in the NMDS ordination (Fig. 3). Considering only the oldest and deepest of the four profiles that were clearly accumulating organic matter, we calculated the vertical accretion rate to be between 0.4 and 4.2 mm yr⁻¹ and the long-term net rate of carbon accumulation (LORCA) to be between 2.7 and 19.2 gC m⁻² yr⁻¹ (Table 4.3).

Profile	Depth	Calibrated ¹⁴ C age (cal. yrs BP)		Carbon	Accretion rate	LORCA
	(cm)	Median Probability	2σ age range	(kg m ⁻²)	(mm yr ⁻¹)	(g m ⁻² yr ⁻¹)
	Forest Lag					
Celery Top Rainf.	60	2350	2155-2680	43.0	2.5	18.3
Moorland	60	1440	1315-1545	27.7	4.2	19.2
	Louisa Plains					
Peat mound Scrub	60	7170	6985-7310	39.0	0.8	5.4
Moorland	30	7215	7005-7415	19.6	0.4	2.7

Table 4.3. The depth, calibrated ^{14}C basal age (see Table 2), mass of accumulated carbon, average rate of vertical accretion and long term net rate of carbon accumulation (LORCA) for the four deepest and oldest organic soil profiles that were clearly accumulating organic matter. Note that estimates of vertical accretion and LORCA were calculated using median calibrated ^{14}C basal age and do not take into account the potential effects of fire on carbon accumulation (see text).

Nutrient status of organic soil profiles

Soil organic carbon was strongly positively correlated with soil nitrogen ($r^2 = 0.74$) and cation exchange capacity ($r^2 = 0.76$), but only weakly positively correlated with soil phosphorus ($r^2 = 0.31$). The depth of the organic soil strongly influenced estimates of total nutrient stocks, because a substantial amount of carbon, nitrogen and phosphorus was stored below 20 cm depth in the deeper soil profiles (Figure 4.6a,b,c). If only the upper 20 cm of the profiles are considered, phosphorus stocks decreased from rainforest through to moorland at both Forest Lag and Louisa Plains (Figure 4.6c), but nitrogen stocks showed no strong decreasing trend at either landscape setting (Figure 4.6b). When the entire profile was considered, phosphorus stocks showed a systematic decrease from rainforest to moorland vegetation at Louisa Plains but not at Forest Lag (Figure 4.6c). Such a decrease was not evident in total nitrogen stocks in the entire profile at either site (Figure 4.6b). Cation exchange capacity showed no systematic trend from rainforest to moorland at either landscape setting when averaged across the upper 20 cm of the soil profile (Figure 4.6d).

Discussion

Can $\delta^{13}\text{C}$ in soil profiles be used to examine boundary dynamics in southwest Tasmania?

$\delta^{13}\text{C}$ values for vegetative material collected in moorland, eucalypt-scrub and rainforest were characteristic of plants that use the C3 photosynthetic pathway (Dawson *et al.*, 2002). Nevertheless, we observed a significant difference in $\delta^{13}\text{C}$ values for vegetative material sampled from moorland species compared to rainforest or eucalypt-scrub species. Differences in $\delta^{13}\text{C}$ values between these C3 vegetation communities could be due to a range of plant physiological characteristics and environmental factors such as light, nutrient and water

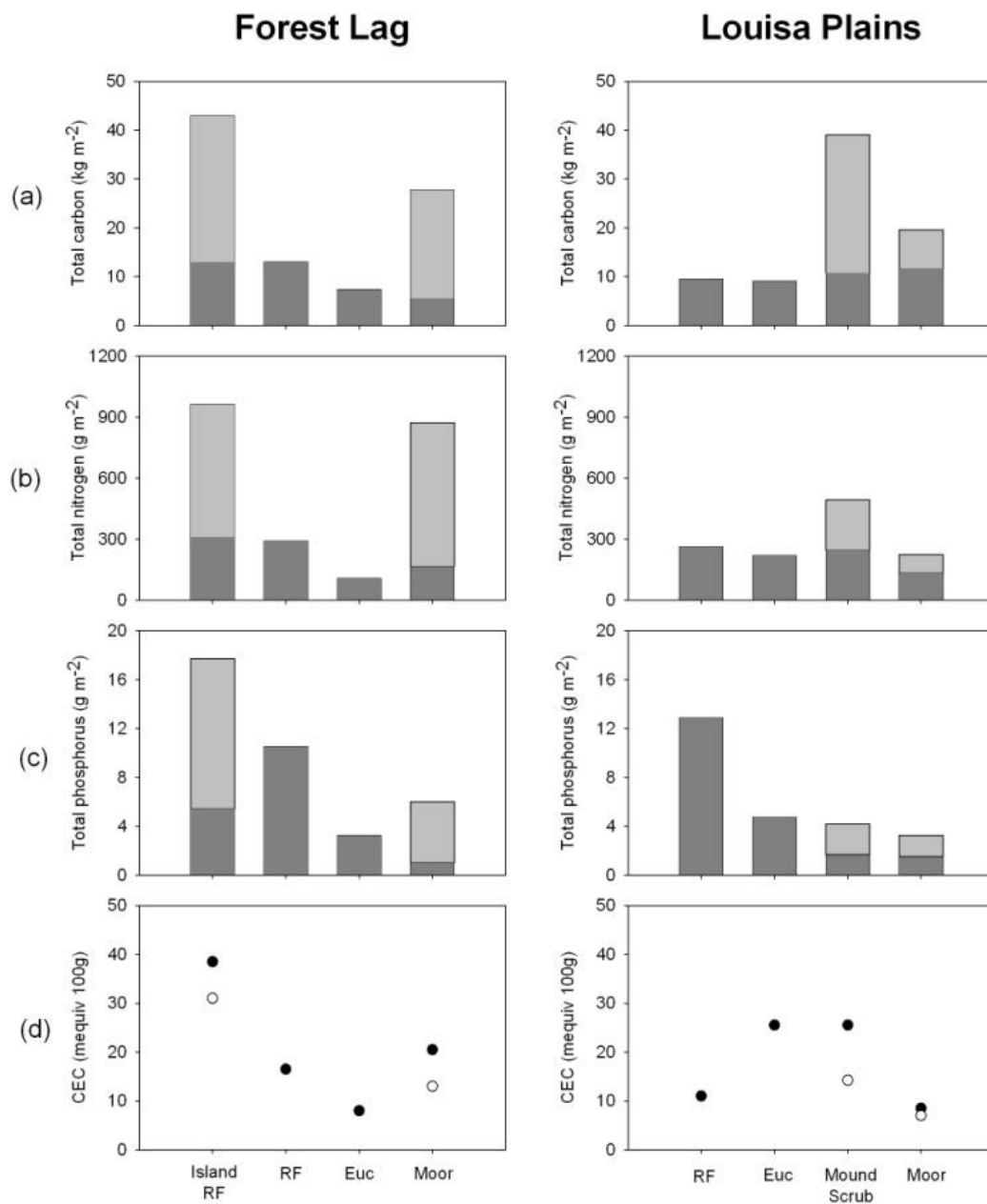


Figure 4.6. The estimated mass of soil organic carbon (a) nitrogen (b) and phosphorus (c) in the upper 20cm (common to all profiles; dark grey shading) and to the full depth (light grey shading) of each organic soil profile sampled from Forest Lag and Louisa Plains. Mean Cation Exchange Capacity (CEC) for the upper 20cm (solid circle) and the lower profile (open circle) is shown in (d). Profiles are arranged left to right from rainforest (RF) through eucalypt (Euc) and sclerophyll scrub (Scrub) to moorland (Moor).

availability (reviewed by O'Leary, 1995; Heaton, 1999; Dawson *et al.*, 2002). The magnitude of the difference between the $\delta^{13}\text{C}$ values of vegetative material ($<3\text{‰}$) and partially decomposed surface litter ($<1\text{‰}$) sampled in each vegetation community was small compared to those found in most investigations of boundary dynamics undertaken in adjacent grassland - forest ecosystems (e.g. Boutton *et al.*, 1998; Bowman and Cook, 2002; Bowman *et al.*, 2004; Krull and Bray, 2005). This lack of variation in $\delta^{13}\text{C}$ of organic matter inputs to the soil resulted in relatively constant $\delta^{13}\text{C}$ values for soil organic matter down the profile and between vegetation communities. As such, we conclude that stable carbon isotopes in soil organic matter cannot be used as an indicator of the vegetation transitions in the moorland-forest mosaics in southwest Tasmania.

Long term net rate of carbon accumulation

Soil organic carbon constitutes an important component of the global terrestrial carbon cycle (Gorham, 1991; Turunen *et al.*, 2002) and it is therefore imperative to characterise both the stores and fluxes of carbon to and from organic soils (Clymo, 1984). Di Folco (2007) recently estimated the extent, amount and distribution of soil organic carbon stocks in Tasmania and our data on basal age and carbon stocks provide a unique opportunity to calculate preliminary estimates of temporal soil carbon dynamics in southwest Tasmania. Estimates of the age, depth and the average vertical accretion rate for the four oldest and deepest organic soil profiles that were clearly accumulating organic matter at Forest Lag and Louisa Plains (1440 yrs to 7215 yrs; 0.3 to 0.6 m; 0.4 to 4.2 mm/yr⁻¹; Table 4.3) are generally less than other Holocene-age profiles in west and southwest Tasmania, including a peat mound at Melaleuca (7920 yrs at 2.0 m; 2.5 mm yr⁻¹; Macphail *et al.*, 1999) and an organic soil profile at Strahan (10,032 yrs at 3.2 m; 3.2 mm yr⁻¹; Fletcher and Thomas, 2010b). The soil profiles investigated at Melaleuca (Macphail *et al.*, 1999) and Strahan (Fletcher and Thomas, 2010b)

included a temporal series of ^{14}C radiocarbon dates throughout each profile which indicated that accumulation rates were affected by significant hiatuses presumably due to the loss of organic soil from burning (Fletcher and Thomas, 2010a; Thomas *et al.*, 2010). Indeed, comparison of the mid-layer and basal ^{14}C dates for the profiles studied here (Figure 4.2; Table 4.2) reveal that soil accumulation is not linear, thus confirming that carbon accumulation is probably influenced by the effects of organic soil removal by fire, and to a lesser extent, oxidation during dry periods. As such, we acknowledge that our estimates of accumulation rates and LORCA are inherently simplified and can only be considered first approximations of carbon accumulation in these soils.

Estimates of LORCA for southwest Tasmania (2.7 to $19.2 \text{ g m}^{-2} \text{ yr}^{-1}$) are at the lower end of the range of LORCA calculated for peatland systems in the Northern Hemisphere boreal zone ($5 - 86 \text{ g m}^{-2} \text{ yr}^{-1}$, Korhola *et al.*, 1995; $3 - 89 \text{ g m}^{-2} \text{ yr}^{-1}$, Tolonen and Turunen, 1996; $19 - 69 \text{ g m}^{-2} \text{ yr}^{-1}$, Borren *et al.*, 2004). The relatively moderate climate of southwest Tasmania compared to the very cold winters, and short, cool to mild summers in the boreal zone is likely to be an important contributing factor to lower accumulation rates. The reasons for regional variations in accumulation rates for even the most intensively studied peatland systems in the Northern Hemisphere are only partly understood (Korhola *et al.*, 1995; Turunen *et al.*, 2002). Indeed, distinguishing the causal factors that explain the low rates of carbon accumulation in southwest Tasmania is difficult given our small dataset and the considerable research effort and expense required to obtain a truly representative set of basal dates for the region. Above all, accounting for the removal of organic matter by past fires on accumulation rates is particularly challenging in these systems (Thomas *et al.*, 2010) but is central to considerations of the carbon storage potential of southwest Tasmanian organic soils.

There is scant published data on the nutrient status of southwest Tasmanian organic soils (reviewed by Jackson, 2000; see also Keith, 1995) and the nature and characteristics of these organic soils have received little attention (but see Bowman *et al.*, 1986; Jarman *et al.*, 1988; Pemberton, 1989; Bridle and Kirkpatrick, 1997) until a recent and comprehensive investigation by di Folco (2007) which, to date, remains unpublished. Therefore, our dataset, although limited in geographic coverage and replication, provides important insights into the processes involved in the development of southwest Tasmanian organic soils. The mass of soil phosphorus in the upper 20 cm of the soil profiles decreased systematically from rainforest through eucalypt to moorland in both landscape settings, but the same decreasing trends were not apparent for the mass of nitrogen or for cation exchange capacity. The trend of decreasing phosphorus across the forest – moorland mosaic offers some support to Jackson's (1968) hypothesis that fire frequency is a significant driving force of soil variation, either directly by reducing soil mass and soil nutrients, or indirectly through its effect on modifying the overlying vegetation (Harwood and Jackson, 1975; Bowman and Jackson, 1981; Jackson, 2000). These results are consistent with the findings of Bowman *et al.* (1986), who linked trends in phosphorus and other nutrient concentrations in organic soils across a similar vegetation boundary in southwest Tasmania with inferred fire frequency and the differing physiology of the constituent vegetation types.

There was other evidence that vegetation type and fire frequency influence organic matter accumulation and nutrient capital in these forest-moorland mosaics. The second axis of the ordination (Figure 4.3) revealed a continuum of soil organic matter attributes amongst the four older organic soil profiles. This continuum followed a gradient of vegetation type from moorland, through scrub, to the rainforest on Celery Top Island and was related to a general

increase in accumulated soil carbon and soil nutrient capital (Figure 4.6). It is particularly pertinent that the highly productive Celery Top Island rainforest supports one of the deepest organic soil profiles with the highest stocks of carbon and nutrients, given that the fire protection afforded by the waters of Bathurst Harbour makes it one of the classic exemplars of long unburnt rainforest in southwest Tasmania. This is well illustrated by the shallow (30 cm) Louisa Plains moorland profile, which had substantially lower carbon and nitrogen stocks than the adjacent deep (60 cm) peat mound scrub profile, despite a very similar period of accumulation (~7200 yrs; Figure 4.2). These inverse relationships between the frequency of fire and the accumulation of organic matter and nutrients may contribute to the positive feedbacks between vegetation, fire and soil that underpin the Jackson (1968) model (but see Chapter 3 Discussion).

Our data on organic soil depth, age and accumulated carbon are concordant with the findings of di Folco (2007) that the nature and characteristics of organic soils across the landscape may be the result of an interaction with not only vegetation and fire frequency, but also other environmental factors such as drainage conditions and topography. With the exception of the rainforest on Celery Top Island, the soil profiles in the forested communities were distinctly shallower, contained less organic matter and had more recent ^{14}C basal dates than the moorland and scrub profiles. We suggest that these differences may be partly explained by the combined effects of vegetation and topography on local drainage conditions. The Louisa Plains moorland and peat mound scrub profiles were located on a terraced floodplain (Figure 4.2) that experiences a periodically raised watertable. At Forest Lag, the moorland profile was located at the foot of a slope and the Celery Top Island profile was situated in a localised depression. It is possible that waterlogged conditions in these topographic settings impede aerobic decomposition resulting in low levels of oxidation, hence the net accumulation of deep profiles of organic matter at these sites over thousands of years. Conversely, the soils

found under the rainforest and eucalypt forest were relatively well aerated because of their topographic position on well drained slopes or convex ridgetops and the effects of transpiration from an overstorey of mature trees (Figure 4.2). Consequently, these profiles may be characterised by a relatively fast turnover - or cycling - of organic matter. Supporting these observations, di Folco (2007) found that slope and topography were important variables influencing the amount of organic matter accumulated in Tasmanian organic soils through their effect on drainage patterns and the water table. Furthermore, Macphail *et al.* (1999) and Brown and Podger (1982a) noted the relationship between drainage and soil organic matter accumulation at Louisa Plains and Forest Lag respectively. These observations of linkages between topography, drainage and organic soil characteristics may contribute to the suite of physical environmental factors that Mount (1979) put forward as key influences on the perceived stability of vegetation patterns in this landscape. The idea that vegetation and fire patterns are a consequence of landscape setting was recognised by Jackson (1968) but emphasised by Mount (1979) and further investigation is required to understand the relative importance of these edaphic factors.

Do nutrient-poor moorland soils inhibit the development of woody vegetation?

The estimates of phosphorus stocks in the two moorlands studied here (32 and 59 kg ha⁻¹; Figure 4.6c) exceed the threshold amount of phosphorus required for the development of woody forest vegetation (20-30 kg ha⁻¹; Bond, 2010). According to these guidelines, it appears that soil phosphorus alone does not limit the establishment of woody vegetation in southwest Tasmanian moorlands (see Chapter 3 Discussion). Consequently, phosphorus may not act as a barrier to the vegetation transitions that Jackson (1968) predicted in the long absence of fire. Indeed, Bond (2010) found that nutrient stocks rarely constrained forest development in savannahs and heathlands in South America, Africa and in the southwest of

mainland Australia. Of course, the applicability of the threshold values calculated by Bond (2010) to southwest Tasmanian ecosystems is debatable, but unfortunately the current information on above and belowground nutrient stocks for this region are scarce and insufficient for calculating thresholds specific to southwest Tasmania.

Conclusions

Our study provides an important palaeoecological context to our understanding of the formation of the organic soils and fire patterned vegetation of southwest Tasmania. We found that high resolution historical ecology methods involving stable carbon isotopes are inappropriate in this landscape. Our results – whilst preliminary - suggest that the nature and characteristics of organic soils across the landscape are the result of an interaction with not only vegetation and fire frequency, but also other factors such as drainage conditions and topography. Our data suggest that the amount of phosphorus in moorlands soils may not limit woody vegetation development. Collectively, our results highlight the complexity of soil - vegetation patterns in this region and lend tentative support for some of the concepts inherent in two ecological models proposed to explain the existence and maintenance of the fire patterned vegetation mosaic. Clearly, a series of targeted and well replicated studies of organic soils in southwest Tasmania are required to untangle this complexity.

Chapter 5: Age and growth of a fire prone Tasmanian temperate old-growth forest stand dominated by *Eucalyptus regnans*, the world's tallest angiosperm

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Abstract

Forests are key components of the global carbon cycle, with deforestation being an important driver of increased atmospheric carbon dioxide. Temperate old-growth forests have some of the highest above ground stores of carbon of any forest types on Earth. Unlike tropical forests, the ecology of many temperate forests is dominated by episodic disturbance, such as high intensity fire. An exemplar of a particularly carbon dense temperate forest system adapted to infrequent catastrophic fires is the *Eucalyptus regnans* forests of south eastern Australia. Knowledge of the growth and longevity of old-growth trees is crucial to understanding the carbon balance and fire regimes of these forest systems. In an old-growth *E. regnans* stand in the Styx Valley in southern Tasmania we used dendrochronological techniques and radiocarbon dating to determine the age and stem growth of *E. regnans* and *Phyllocladus aspleniifolius*, an understorey rainforest conifer. Our analysis revealed that an even-aged cohort of *E. regnans* and *P. aspleniifolius* established in 1490-1510AD, apparently after a stand-replacing fire. The stem growth rates of *E. regnans* in the first 100 years were very rapid compared to the co-occurring *P. aspleniifolius*. That the longevity of *E. regnans* is > 500 years challenges the suggested 350-450 year timeframe proposed for the widely held model of succession from eucalypt to rainforest. These forests not only have the potential to store vast amounts of carbon, but can also maintain these high carbon densities for a long period of time. Estimates of the capacity of these forests to sequester and store carbon should explicitly consider past harvesting and fire regimes and the potential increases in the risk of fire associated with climate change.

Introduction

Forests are of prime importance to the global carbon cycle, with deforestation since industrialisation contributing about 20% of the increased carbon dioxide (CO₂) in the atmosphere (IPCC, 2007; Bowman *et al.*, 2009). There is an obvious need to reduce tropical deforestation in order to mitigate the effects of anthropogenic climate change (Skole and Tucker, 1993; IPCC, 2007), although attention is now also turning to the remaining old-growth forests outside the tropical zone. Recent reviews have found that old-growth temperate forests may constitute a substantial and largely neglected carbon sink (Luyssaert *et al.*, 2008) and that estimates of biomass carbon densities in mature or primary forests are much higher for temperate moist forests than for tropical or boreal forests (Keith *et al.*, 2009). Yet, unlike tropical rainforest systems, the ecology of many temperate forests is dominated by episodic disturbance by fire (Agee, 1993; Attiwill, 1994). Thus the extra-ordinary carbon storage of old-growth temperate forest ecosystems is more apparent than real because the fires that maintain them result in a periodic efflux of carbon. A comprehensive understanding of the global carbon cycle must therefore include an understanding of the fire regimes that maintain temperate forests.

The advent of satellite imagery in the late 20th century has revolutionised our understanding of fire activity on Earth (Flannigan *et al.*, 2009) and enabled detailed characterisation of fire regimes in frequently burnt areas such as tropical savannas (Russell-Smith *et al.*, 2003). In forests where the return time of fires is considerably longer, the quantification of fire regimes requires historical reconstructions of fire events, usually through dendrochronological techniques (Fritts and Swetnam, 1989; Bowman, 2007). Dendrochronological studies of post-fire cohorts have enabled the characterisation of fire regimes for a range of high-biomass, old-growth temperate forests that experience high-severity, stand-replacing fire events at very

long intervals (e.g. Hemstrom and Franklin, 1982; Silla *et al.*, 2002; Winter *et al.*, 2002). Old-growth *Eucalyptus regnans* forests appear to conform to the pattern of infrequent and intense stand replacing fires, yet the precise dates of pre-European fire events which are crucial for characterising the fire regimes of these forests remain largely unknown (McCarthy *et al.*, 1999; Simkin and Baker, 2008), reflecting an Australia-wide paucity of dendrochronological studies (Pearson and Searson, 2002) and difficulties in applying classical dendrochronological techniques to eucalypts (Brookhouse, 2006). Understanding the return times of stand-replacing fires in *E. regnans* forests and their relationship with prevailing climatic conditions is critical for contextualising catastrophic fire events in south eastern Australia, such as the recent February 2009 ‘Black Saturday’ fires that burnt vast areas of forest in Victoria, south eastern Australia, with the loss of 173 lives and more than 3000 homes.

High-severity ($> 800 \text{ kW m}^{-1}$) fires are crucial for the regeneration of *E. regnans* forests that occur in high rainfall regions of Tasmania and Victoria (Ashton, 1981; Attiwill, 1994). An established ecological generalisation that is the basis of current silvicultural practice, is that *E. regnans* forests predominantly form single-age cohorts that arise following stand replacing fires (Gilbert, 1959; Ashton, 1976; Attiwill, 1994), although multi-aged stands are not uncommon, developing after fires that kill only a fraction of the stand (McCarthy and Lindenmayer, 1998; Lindenmayer *et al.*, 1999; Turner *et al.*, 2009). *E. regnans* is not only the world’s tallest flowering plant, but it is also unusual among the eucalypts in its sensitivity to fire. *E. regnans* is afforded limited protection from fire from its thin bark and the lack of a lignotuber makes for limited vegetative recovery following severe fire damage (Ashton, 1976, 1981). Regeneration is very limited in the absence of fire so *E. regnans* is aptly described as the world’s largest obligate seeder. This peculiar biology has far reaching implications for the population ecology of this species. Single-aged cohorts of *E. regnans* are

vulnerable to demographic collapse if fire intervals are shorter than the time to reach reproductive maturity. Likewise where fire intervals exceed the lifespan of the youngest cohort of *E. regnans*, the stand would be replaced by rainforest species that are able to regenerate without fire disturbance. In sum, the *E. regnans* system is held in a delicate balance by fire return intervals (Jackson, 1968). Despite being integral to their persistence in the landscape, there remains considerable uncertainty regarding the growth rates and longevity of *E. regnans* forests and thus the potential of this species to survive under varying fire frequencies. These questions are of considerable interest because they provide a temporal context for understanding the dynamics of carbon storage in *E. regnans* forests which have the highest known biomass carbon density of any forest in the world (Keith *et al.*, 2009).

The purpose of this study is to characterise the age and pattern of stem growth of a stand of old-growth *E. regnans* in southern Tasmania. Our approach is to estimate the age and growth rates of co-occurring cohorts of *E. regnans* and *Phyllocladus aspleniifolius* (an understorey rainforest conifer) in an old-growth forest stand by applying a range of mutually reinforcing and independent dating techniques, namely; cross-dating of both *E. regnans* and *P. aspleniifolius* tree-ring series using dendrochronological techniques (Fritts, 1976; Fritts and Swetnam, 1989) and radiocarbon dating of sections of these cross-dated tree-ring series (Hua, 2009). *P. aspleniifolius* has been shown to be suitable for dendrochronological reconstructions using classical cross-dating techniques (Allen *et al.*, 2001) but previous attempts to cross-date *E. regnans* have not been successful (Brookhouse, 2006; Simkin and Baker, 2008). We then use our findings to (a) evaluate previous estimates of the age of old-growth *E. regnans* trees (b) consider the implications for the model of forest succession proposed for *E. regnans*-rainforest systems and (c) consider the implications for the fire regimes and carbon storage of *E. regnans* forests.

Methods

Study Area

The study was located in the Styx Valley in the southern Forests of Tasmania (Figure 5.1a). The region experiences a mean annual rainfall of approximately 1175mm, with a mean minimum and maximum annual temperature of 5.3 and 16.1 °C respectively (Australian Bureau of Meteorology, June 2009). The eucalypt forests of the Styx Valley are renowned for the presence of large numbers of giant trees that exceed 85 m in height. The forests of this region are comprised of a mosaic of (a) cool temperate rainforest dominated by *Nothofagus cunninghamii* and *Atherosperma moschatum*, (b) tall eucalypt forests with dense multi-layered understoreys dominated by rainforests species (mixed forests) or broadleaved shrubs and small trees (wet sclerophyll forests) and (c) managed production forests and plantations.

The study area was situated in a forest stand on a gently undulating plateau south of the Styx River that was harvested between December 2007 and February 2008 (Figure 5.1b). The study site was chosen because it was an excellent example of an old-growth 'mixed' forest, having a low stocking of very tall *E. regnans* (height 55-75m with 50-70% crown cover) emergent from a dense rainforest composed of *N. cunninghamii* and *A. moschatum* with *P. aspleniifolius*, *Eucryphia lucida* and *Anodopetalum biglandulosum* (see Figure 5.2). The absence of cut stumps or fire scars intimated that the stand was undisturbed by past harvesting activities or recent fire.

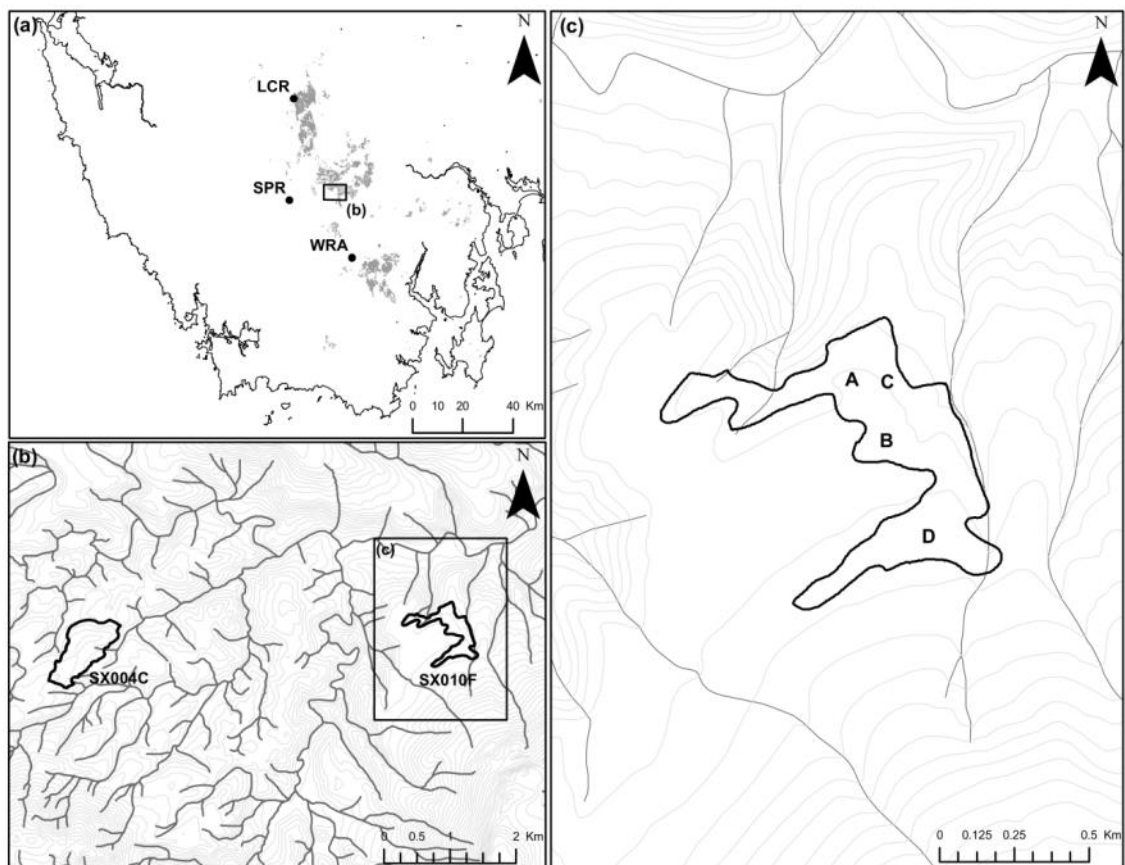


Figure 5.1. Study locations for the Styx Valley dendrochronology study in the southern forests of Tasmania. (a) The distribution of *Eucalyptus regnans* forests in southern Tasmania (shaded), the location of the current study in the Styx Valley (box) and three *Phyllocladus aspleniifolius* stands for which previously published tree-ring chronologies are available (LCR: Lower Cole Road, SPR: Scotts Peak Road, WRA: Warra; Allen *et al.*, 2001, Allen, 2002). (b) Locations of the study areas in the Styx Valley used by Dean and Roxburgh (2006) for biomass carbon estimation (SX004C) and for dendrochronological investigations in this study (SX010F). (c) Locations of sampling sites for *E. regnans* (A) and *P. aspleniifolius* (B), and the diameter survey plots (C and D) within the mapped photo-interpreted vegetation class (solid line).



Figure 5.2. Old-growth *Eucalyptus regnans* stand with rainforest understorey in the Styx Valley in southern Tasmania sampled for dendrochronological analysis in this study.

Stand structure measurements and sampling of stem discs.

Fieldwork occurred during the harvesting program, thus constraining baseline measurements, so the stand structure was determined by measuring tree diameters within two 1.3 ha⁻¹ plots immediately adjacent to the area where stems were sampled (Figure 5.1c). Within each of these plots stem diameters were measured at breast height over bark at 1.3m above ground level (DBH) for all live eucalypts >10cm DBH. Where trees were heavily buttressed, diameters were measured or as high as practical on the bole (i.e. Turner *et al.*, 2009).

Collection of material for dendrochronological analysis was constrained by the practicalities of sampling very large trees (see Figure 5.2) with pronounced buttressing, very hard dense wood and ubiquitous internal stem rot. Harvesting of this stand enabled collection of stem sections that weighed up to 300kg from felled trees. This approach carried numerous practical and safety constraints associated with working closely with a harvesting operation and meant that ideal sampling strategies (i.e. sampling at consistent heights) and coring of large numbers of trees across multiple sites was impossible.

For each *E. regnans* tree selected for dendrochronological analysis, the DBH was determined prior to felling. Following felling, the interior of each stem was inspected for rot and stem discs were taken from eighteen trees at the point where the wood was sound with clearly visible centre rings (between 6.0 and 20.0 m above ground). Stem discs at ‘stump height’ (0.5m to 1.0m) were acquired from twenty-four *P. aspleniifolius* trees from a small grove that was harvested in January 2008 (Figure 5.1c). It was not possible to collect data on the size class distribution of *P. aspleniifolius* given the patchy occurrence of this species and safety issues associated with working in an area that was being harvested.

Chronology development

Depending on the size of the disc, each of the *E. regnans* discs were sectioned into two or four equally spaced radial segments of 200mm width and polished with progressively finer grades of sandpaper. Series of ring widths were measured to the nearest 0.01mm along each radii using a measuring stage and microscope. The program COFECHA was used to develop a mean chronology from the measured tree-ring series and to facilitate the identification of measurement of cross-dating errors (Holmes, 1983; Grissino-Mayer, 2001). Most radii exhibited wide rings with relatively distinct (albeit diffuse) earlywood and latewood boundaries for the innermost ~125 rings (including the pith), beyond which measurement and cross-dating of tree rings on most radii became increasingly difficult due to a combination of exceedingly narrow rings, wedging or contortion and indistinct ring boundaries. Therefore, we focussed on the inner 125 rings that could be identified with confidence. When preparing the *E. regnans* chronology, the first ring of the chronology was initially assigned an arbitrary value of 'Year 1' and each series was progressively culled by 5 rings from year 125 backwards until COFECHA mean inter-series correlations exceeded 0.35 for all 30 year segments in the chronology. In effect, this resulted in a 'floating chronology'. The first ring of the *E. regnans* floating chronology was later 'anchored' to the absolute time scale using 'wiggle matching' of a sequence of radiocarbon dates (see following section) and all rings in the chronology were assigned a calendar year relative to this date.

Intact *P. aspleniifolius* discs were sanded and ring widths were measured to the nearest 0.01mm along three radii for each disc. The program COFECHA was used to develop a mean chronology from the measured tree-ring series and to facilitate the identification of measurement of cross-dating errors (Holmes, 1983; Grissino-Mayer, 2001). Unlike *E. regnans*, the process of cross-dating of *P. aspleniifolius* tree-ring series was inclusive of all

rings from the pith to the cambium. Ring wedging is a common phenomenon in *P. aspleniifolius*, resulting in locally absent rings (Allen *et al.*, 2001). Where this was the case the measured radius was temporarily rotated clockwise or anticlockwise until locally absent rings reappeared, then shifted back to the original radius. If rotations from the original radius exceeded 45 degrees we followed Allen *et al.* (2001), where locally absent rings were substituted with the average ring width for other radii from the same tree.

Three previously published *P. aspleniifolius* chronologies from the Southern Forests region (Figure 5.1a) were available to validate the annual resolution of the *P. aspleniifolius* chronology developed in this study. Details of these chronologies were presented in Allen *et al.* (2001) and Allen (2002). All chronologies, including the chronology produced in this study, were detrended using 128-year 50% cut-off cubic smoothing spline (Allen *et al.*, 2001; Allen, 2002). Pearson correlations between all sites for the entire common length of each pair of chronologies were calculated for residual chronologies generated during the detrending process.

Dating of tree rings using radiocarbon dating.

Radiocarbon dating of tree rings was used in this study for two objectives: (1) ‘wiggle matching’ of a sequence of radiocarbon dates was used to anchor the Styx Valley *E. regnans* floating chronology to the calendar time scale (Bronk-Ramsey *et al.*, 2001; Hua, 2009) and (2) bomb ^{14}C radiocarbon was used to independently validate the annual resolution of the Styx Valley *P. aspleniifolius* chronology (Hua, 2009). For the first objective, nine sequential decadal samples were taken from a section of Tree 10 that coincided with years 11-20, 21-30.....91-100 of the *E. regnans* floating chronology for accelerator mass spectrometry (AMS) ^{14}C analysis. For the second objective, wood samples were taken from two single tree rings

that were assigned years 1963AD and 1968AD in the *P. aspleniifolius* chronology for AMS ^{14}C analysis. The samples were pre-treated to alpha-cellulose and converted to graphite following the methods described in Hua *et al.* (2004) and Hua *et al.* (2001). The graphite was analysed for radiocarbon using the STAR AMS Facility at ANSTO (Fink *et al.*, 2004). For each sample, ^{14}C concentration and/or radiocarbon age was determined after corrections for AMS machine background, procedural blank and isotopic fractionation using measured $\delta^{13}\text{C}$. Wiggle matching of ^{14}C radiocarbon dates from *E. regnans* to the SHcal04 calibration curve for the Southern Hemisphere (McCormac *et al.*, 2004) to derive calendar dates was performed using the OxCal (Version 3.10) radiocarbon calibration program (Bronk-Ramsey, 2001). For the two single rings of *P. aspleniifolius*, ^{14}C concentrations were calibrated to calendar ages using the atmospheric bomb ^{14}C data for the Southern Hemisphere zone (Hua and Barbetti, 2004), and the CALIBomb program (Stuiver and Reimer, 1993).

Growth curves

Using the cross-dated chronologies and the results of the radiocarbon dating, all *E. regnans* and *P. aspleniifolius* trees that established contemporaneously were identified. For these trees, cumulative diameter growth at sampling height was reconstructed from cross-dated annual tree-ring width measurements. Average cumulative diameter growth for each species for the first 90 years was calculated from these reconstructions to compare the early growth rates of *E. regnans* and *P. aspleniifolius*. Models were fitted using non-linear least squares regression, to the formula $\text{Diameter} \sim a \times \text{Year}^b$, in which no intercept term was included. These models were used to illustrate growth curves for the entire lifespan of *E. regnans* and *P. aspleniifolius*. Given the non-conventional and inconsistent sampling heights of *E. regnans* trees (6.0 to 20.0 m), we avoided detailed modelling of growth rates and instead focussed on generalised comparisons of stem growth between the two species.

Results

E. regnans stand structure

The diameters of stems used in the dendrochronological analysis were comparable with the diameters of trees in the neighbouring unlogged plots (Figure 5.3). These data indicate that this stand (Figure 5.1c) consists of a single cohort of very large eucalypts. Of the 75 unlogged trees measured, 70 were >140cm DBH with the remaining five <40cm DBH. These smaller trees were geographically constrained to a small area and appear to be associated with individual gap regeneration well after the establishment of the larger cohort.

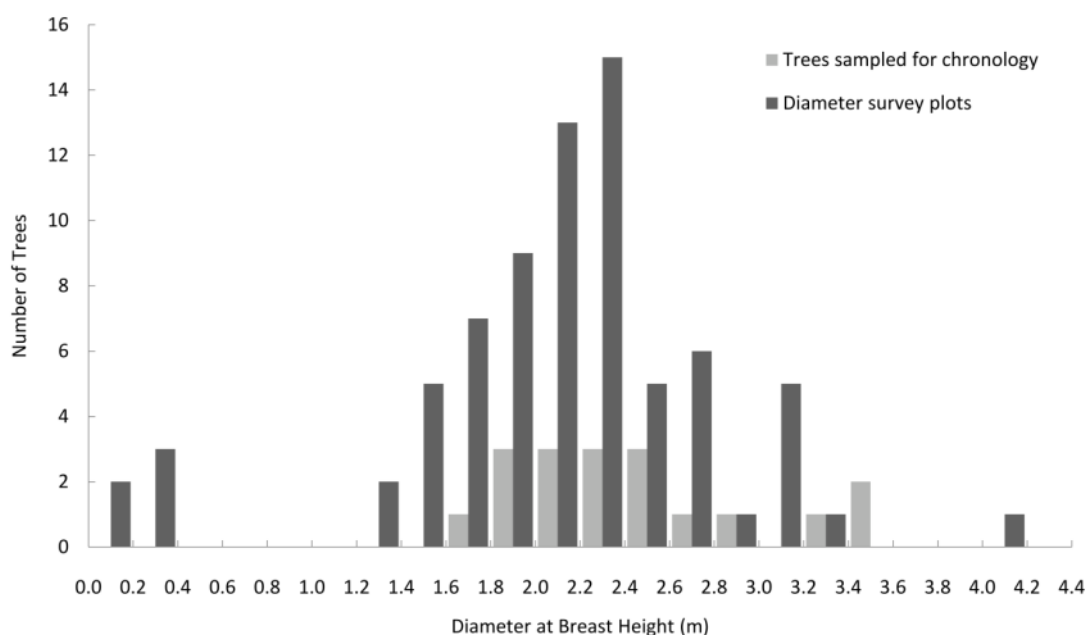


Figure 5.3. Diameter distribution of *Eucalyptus regnans* trees (>10cm DBH) measured in two 1.3ha plots within the Styx Valley forest stand (n=75) and the diameter distribution of *E. regnans* trees used to generate the cross-dated chronology (n=18).

E. regnans dendrochronology, radiocarbon dating and stand establishment dates

Iterative culling of the outermost rings of each tree-ring series included in the Styx Valley *E. regnans* ‘floating chronology’ resulted in an average segment length of 84 years and an overall chronology length of 100 years (Table 5.1). The high mean inter-series correlation of 0.62 calculated by COFECHA suggests a strong common signal between the tree-ring series. The ^{14}C radiocarbon ages obtained for the sequence of cross-dated tree rings from the *E. regnans* chronology and the respective wiggle matched calendar dates are presented in Table 5.2 and illustrated in Figure 5.4. Using data in Table 5.2, the first ring in the floating chronology was back-calculated to be $1512.5 \pm 20.5\text{AD}$ (2σ) and all subsequent rings in the chronology were assigned a calendar year relative to this date.

<i>Statistic</i>	<i>E. regnans</i>	<i>P. aspleniifolius</i>
Period covered	Floating chronology	1511-2006 AD
Length of chronology	100 years	495 years
Number of trees	18	25
Number of series/radii	57	63
Mean Interseries Correlation	0.617	0.604
Average ring width (mm)	31.6	8.0
Average segment length and range (rings)	84 (60-97)	447 (197-492)

Table 5.1. Details of cross-dated tree-ring chronologies developed for *Eucalyptus regnans* and *Phyllocladus aspleniifolius* from the Styx Valley. Mean Interseries Correlation was generated by the dendrochronology program COFECHA (Holmes, 1983; Grissino-Mayer, 2001).

Ring Number	^{14}C age (BP)		Calendar Age (AD)		Lab Code
	Value	1σ	cal AD	2σ	
11-20	335	26	1527.0	20.5	OZL735
21-30	368	28	1537.0	20.5	OZL736
31-40	308	28	1547.0	20.5	OZL737
41-50	348	24	1557.0	20.5	OZL738
51-60	390	31	1567.0	20.5	OZL739
61-70	405	30	1577.0	20.5	OZL740
71-80	357	31	1587.0	20.5	OZL741
81-90	426	31	1597.0	20.5	OZL742
91-100	406	26	1607.0	20.5	OZL743

Table 5.2. ^{14}C radiocarbon ages and wiggle matched calendar age for a sequence of 10-year tree-ring samples from *Eucalyptus regnans* Tree 10. Wiggle matching of radiocarbon dates to the SHcal04 calibration curve for the Southern Hemisphere (McCormac *et al.*, 2004) to derive calendar dates was performed using the OxCal calibration program version 3.10 (Bronk-Ramsey, 2001; Figure 5.4). ^{14}C radiocarbon ages are older for younger wood samples because of the rising trend in the atmospheric ^{14}C between 1500AD-1600AD (Figure 5.4).

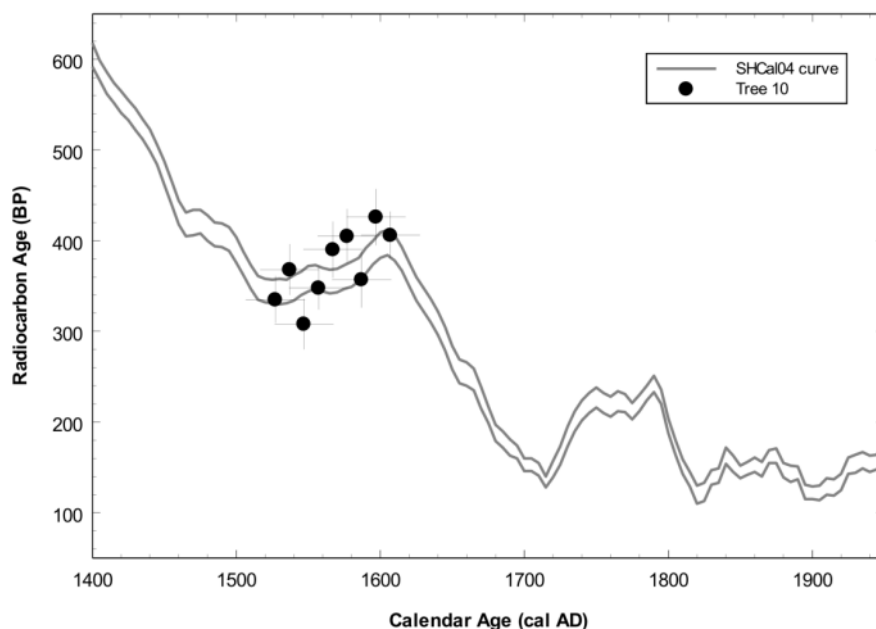


Figure 5.4. Wiggle matching of ^{14}C radiocarbon dates from a series of tree-rings (Tree 10) from the *Eucalyptus regnans* chronology to the SHCal04 calibration curve for the Southern Hemisphere (McCormac *et al.*, 2004). Analyses were performed using the OxCal (Version 3.10) radiocarbon calibration program (Bronk-Ramsey, 2001). SHCal04 curve is plotted in 1σ range. Error bars are 1σ for radiocarbon age and 2σ for calendar age.

The calendar year of the pith for seventeen *E. regnans* trees (Figure 5.5) fell within a 16 year time-span from $1512.5 \pm 20.5\text{AD}$ (2σ) to $1528.5 \pm 20.5\text{AD}$ (2σ). The linear relationship between pith date and sampling height ($R^2 = 0.76$) allowed us to estimate height growth to be approximately 1.0m per year (Figure 5.5). This enabled us to calculate the number of years for each tree to reach its respective sample height, and therefore estimate an approximate establishment date for each tree at ground level. Using this methodology, we estimate that all seventeen *E. regnans* trees established between $1503 \pm 20.5\text{AD}$ (2σ) and $1511 \pm 20.5\text{AD}$.

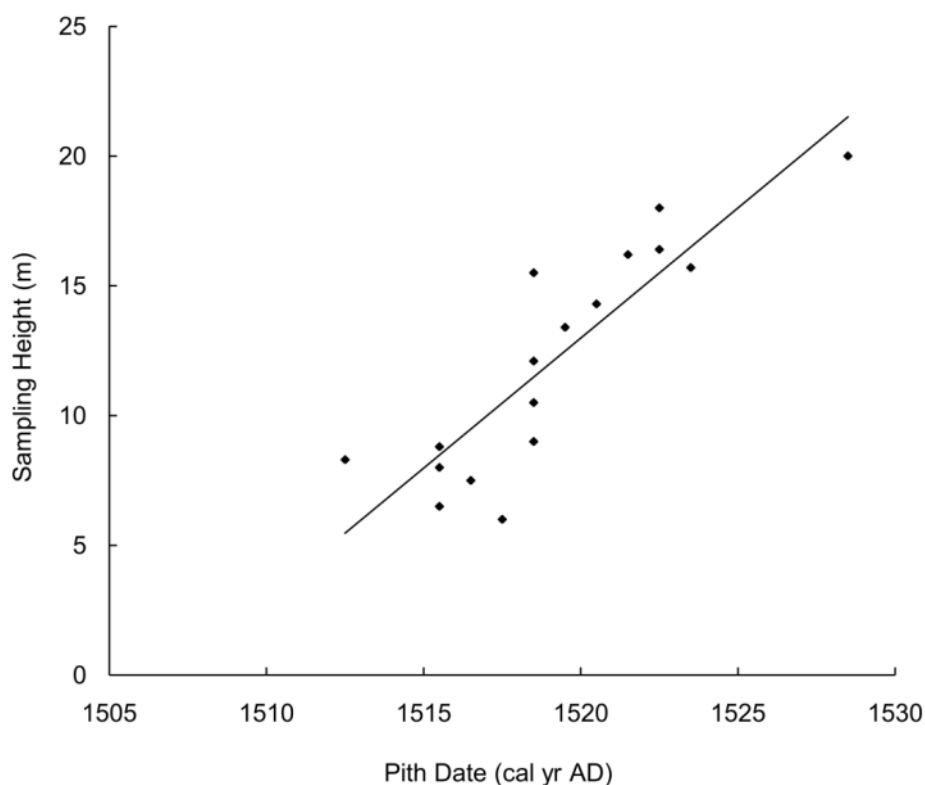


Figure 5.5. The pith date of seventeen *Eucalyptus regnans* trees from the Styx Valley stand and the relationship with sampling height. Pith dates were estimated from the *E. regnans* floating chronology, which was anchored to the absolute timescale (calendar year AD) using wiggle matching of a sequence of radiocarbon dates (see text). The pith dates plotted in this diagram are mean calendar year AD without uncertainties. The relationship between sampling height and pith date (solid line) is given by $y = 1.003x - 1511.6$ ($R^2 = 0.76$, $n = 17$) indicating a height growth of approximately 1.0m per year. Tree 1 was missing the pith and was not included in calculating this figure. The date of the innermost ring for Tree 1 was estimated to be $1528.5\text{AD} \pm 20.5$ (2σ).

P. aspleniifolius dendrochronology, radiocarbon dating and stand establishment dates

The Styx Valley *P. aspleniifolius* chronology spanned 495 years from 1511 to 2006 (Table 5.1). This chronology was supported by a high mean inter-series correlation of 0.60 calculated by COFECHA and consistently high inter-site correlations with three previously published *P. aspleniifolius* chronologies from the Tasmanian Southern Forests region (Figure 5.1a, Table 5.3). The results of the ^{14}C bomb pulse radiocarbon dating (Figure 5.6) provide an independent validation of the annual resolution of the Styx Valley chronology. The pith dates of the *P. aspleniifolius* trees indicate a strong pulse of tree establishment in the early 1500's and a weaker pulse of tree establishment in the mid to late 1600's (Figure 5.7). The chronology revealed that fifteen of the sampled stems reached sampling height between the years 1511 and 1531, and four reached sampling height between the years 1662 and 1672. The declining number of establishment dates after 1725 is an artefact of sampling the largest *P. aspleniifolius* in the stand.

	STYX	SPR	WRA	LCR
STYX	1.00	0.68	0.68	0.77
SPR		1.00	0.68	0.64
WRA			1.00	0.62
LCR				1.00

Table 5.3. Correlation matrix for four *P. aspleniifolius* chronologies from the Tasmanian Southern Forests (Figure 1a): The Styx Valley (STYX: this study), Scotts Peak Road (SPR: Allen *et al.*, 2001), Lower Cole Road (LCR: Allen *et al.*, 2001) and Warra (WRA: Allen, 2002). Pearson correlations between all sites for the common length of each pair of chronologies were calculated for residual chronologies generated following detrending.

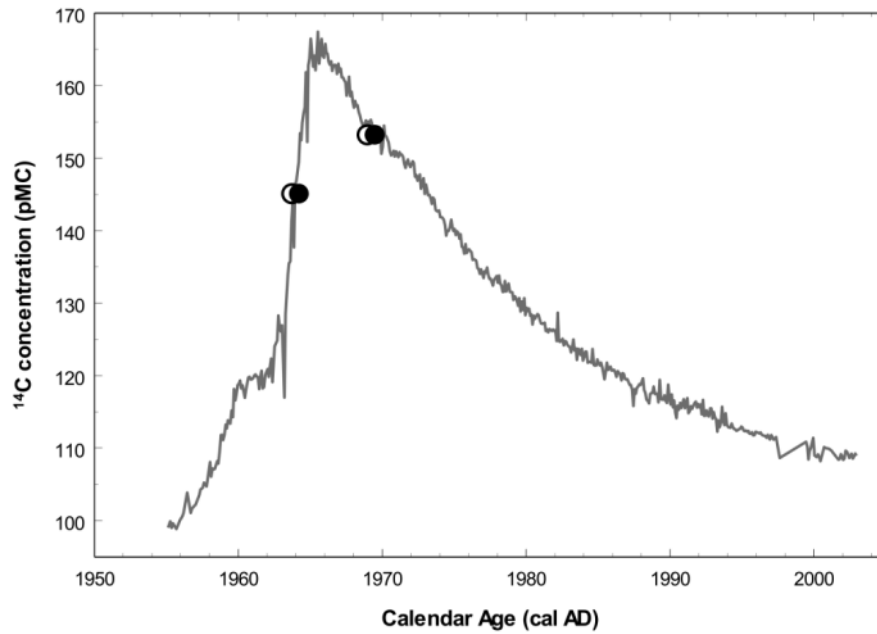


Figure 5.6. Temporal positions of two tree-rings (1963AD and 1968AD) from the *P. aspleniifolius* chronology based on dendrochronology (open symbols) and bomb-pulse ^{14}C dating (solid symbols). These symbols should be plotted in the same positions. However, they are displayed with small temporal offsets for reason of clarity. The grey line is the atmospheric bomb ^{14}C curve for the Southern Hemisphere (Hua and Barbetti, 2004).

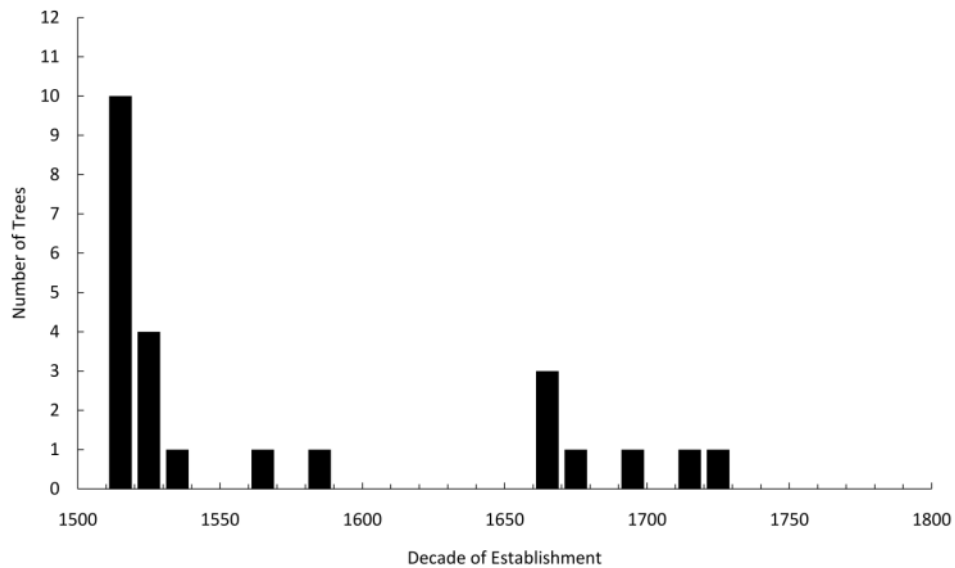


Figure 5.7. Establishment history for *P. aspleniifolius* trees from the Styx Valley stand based on pith dates derived from the cross-dated tree-ring chronology. The decreasing number of establishment dates after 1750 is an artefact of the targeting of large trees >50cm DBH for this study.

Comparison of E. regnans and P. aspleniifolius growth curves

We identified seventeen *E. regnans* trees (Figure 5.8) and fifteen *P. aspleniifolius* trees (Figure 5.7) that had pith dates indicating regeneration in the early 1500's. Modelled growth curves in Figure 5.8 illustrate much more rapid early diameter growth for *E. regnans* compared to *P. aspleniifolius*. At age 25, *E. regnans* attained a diameter approximately 5 times greater than *P. aspleniifolius* and at age 90, diameter was approximately 3 times greater. Almost 45% of the total diameter of the ~500 year old *E. regnans* trees is achieved in the first 90 years of growth.

Discussion

Given the stand structural data (single cohort), and the congruence between the establishment dates of the earliest *P. aspleniifolius* cohort (1511AD – 1531AD) and the estimated establishment date of the *E. regnans* cohort (1503AD - 1511AD \pm 20.5 (2 σ)), we conclude that the Styx Valley study site comprises an even-aged cohort of *E. regnans* established following a stand-replacing disturbance event before 1511AD and probably within the period 1490-1510AD. Given the importance of fire in the regeneration ecology of *E. regnans* (Gilbert, 1959; Ashton, 1976, 1981; Attiwill, 1994), there is little doubt that the cause of this regeneration event was a stand-replacing fire. This conclusion is consistent with that of a number of past studies which have suggested that some areas of old-growth forests in southern Tasmania may have regenerated after fire “in the early 1500's” (Gilbert, 1959; Hickey *et al.*, 1999; Alcorn *et al.*, 2001; Allen, 2002). These previous studies were based on ring counts of eucalypt stumps in the field and the age of a limited number of individual *P. aspleniifolius* trees from cross-dated chronologies that were developed for dendroclimatology research rather than for identifying post-fire cohorts. The methods employed by these studies

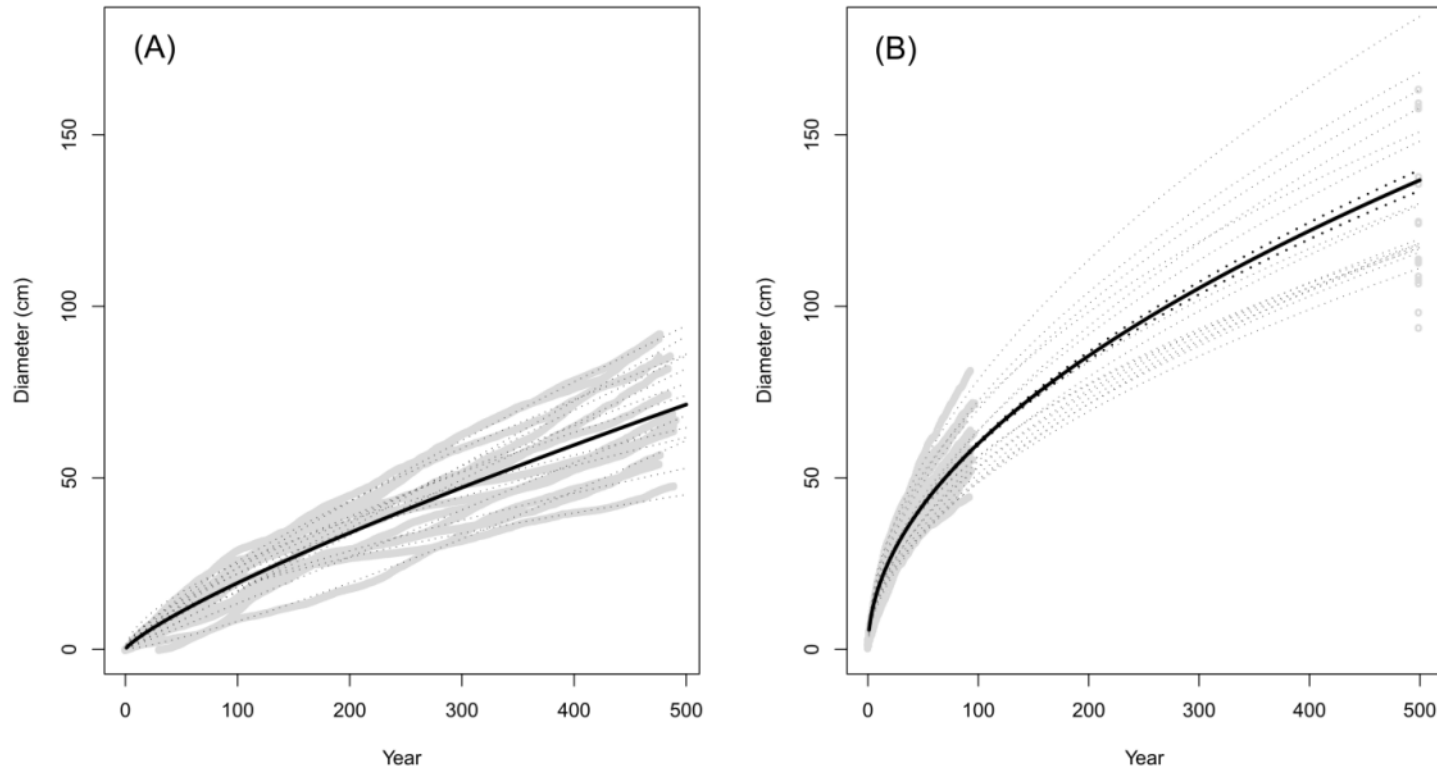


Figure 5.8. Diameter growth curves for co-occurring (a) understorey *Phyllocladus aspleniifolius* and (b) overstorey *Eucalyptus regnans* trees established after a stand replacing fire in the Styx Valley in 1490-1510AD. Growth curves for each tree (solid grey lines) are for cumulative diameter growth at sampling height (PA: 0.5-1.0 m, ER: 6.0-20.0 m) and were reconstructed from cross-dated, annual tree-ring width measurements. The upper limit of growth of *E. regnans* was constrained by disc diameter measurements on trees assumed to be 500 years old. Models were fitted using non-linear least squares regression, to the formula $Diameter \sim a * Year^b$, in which no intercept term was included. Curves were fitted for each tree and for all trees of each species together. Standard errors for the combined curves are indicated with dotted lines.

are of far less reliability than the approach we used here, and therefore, we provide the first robust identification of a pre-European fire event in the southern forests of Tasmania. We conclude that *E. regnans* has a longevity that may exceed 500 years given that observations of the sampled trees indicated that they were not completely senescent (Figure 5.2). Consequently, our findings challenge the commonly held view that the longevity of *E. regnans* is around 350-450 years (Gilbert, 1959; Jackson, 1968; Wells and Hickey, 1999).

Gilbert (1959) and Jackson (1968) proposed that if the period between two fires exceeds the lifespan of *E. regnans*, the eucalypts will be eliminated and replaced by ‘climax’ rainforest, because shade intolerant *E. regnans* seedlings cannot survive in the low light intensity under the rainforest canopy. Our data contributes to current understanding of the temporal dynamics of the Gilbert-Jackson model in two ways. Firstly, the revised longevity for *E. regnans* suggests that the proposed transition to rainforest would take more than 500 years for a single cohort stand. Secondly, by contrasting the comparatively rapid post-disturbance growth rates of *E. regnans* with the concurrently growing *P. aspleniifolius* we illustrate the mechanism whereby the light demanding *E. regnans* can form an upper stratum to compete against the slow-growing and continuously regenerating rainforest understorey. These contrasting ‘tortoise and the hare’ growth rates support the view of Bond (1989) that tree growth rates in the regeneration niche are crucial to understanding the stand dynamics of many mixed angiosperm and gymnosperm forests and are consistent with the model of single cohort, mixed species stands proposed by Oliver and Larson (1996) and Franklin *et al.* (2002). The rapid initial growth of *E. regnans*, where almost half the total stem diameter growth occurs in the first 90 years, forms the basis for the proposed silvicultural rotation times for these forests (i.e. 90 years, Whiteley, 1999). Beyond 90 years we have no data on annual stem diameter growth for *E. regnans*. Sillett *et al.* (2010) report that the growth rate of the lower stems of *E. regnans* trees decreases (or does not change) with increasing age (from 80 years up to 299

years old), yet the upper stems and crown continue to increase growth regardless of age. Regardless of growth rates, *E. regnans* trees achieve a size and longevity rivalled by only the evergreen coniferous forests of the Pacific Northwest of the USA (Waring and Franklin, 1979).

An assumption of the Gilbert-Jackson model of forest succession is that the forests are made up of a single cohort of overstorey eucalypts. While the stand we studied conforms to this assumption, it appears that single cohort forest stands are the exception rather than the rule in old-growth *E. regnans* forests (Lindenmayer *et al.*, 2000b; Lindenmayer, 2009; Turner *et al.*, 2009). Turner *et al.* (2009) used diameter distributions to infer stand ages and variation in cohort structures in unlogged contemporary southern Tasmanian wet eucalypt forests. They found that for pure *E. regnans* stands with trees assumed to be > 110 years old, only 15% were comprised of a single cohort, and inferred that the average time since stand replacing fire for these stands was approximately 230 years. The rarity of >110 year old, single-cohort *E. regnans* stands in the landscape, combined with the longevity of the dominant trees (> 500 years), implies that there is currently a limited capacity for widespread succession of *E. regnans* forest to rainforest in southern Tasmania under current fire regimes. Whether fire regimes and the age structure of these forests, and thus the likelihood of succession, were different under Aboriginal management remains uncertain.

Our data confirm that at least some parts of the Tasmanian forest landscape can be characterised by a fire regime of high-severity, stand-replacing fires with a return time of >500 years. A range of temperate forest stands throughout the world have been shown to have developed from stand-replacing fires over 450 years ago in the Pacific Northwest (Hemstrom and Franklin, 1982; Agee, 1993; Winter *et al.*, 2002; Weisberg and Swanson, 2003) and Rocky Mountains (Romme and Knight, 1981; Kipfmueeller and Baker, 2000;

Buechling and Baker, 2004) regions of North America and in Northern Patagonia in South America (Lara *et al.*, 1999; Veblen *et al.*, 1999). By analysing long-term regional patterns of fire events in relation to long-term reconstructed climate variation, several of these studies have been able to identify climatic conditions conducive to regional stand replacing fire events (e.g. Hemstrom and Franklin, 1982; Veblen *et al.*, 1999; Weisberg and Swanson, 2003; Buechling and Baker, 2004). In Tasmania, analyses of short term (1952-2002) relationships between fire and climate revealed that summer rainfall and indices of the El Nino-Southern Oscillation are important climatic factors influencing the area burnt each summer (Nicholls and Lucas, 2007). Simkin and Baker (2008) demonstrated the use of dendrochronology for precisely determining recent fire events in wet sclerophyll *E. regnans* forests of Victoria (i.e. the 1939 'Black Friday' fires). Our study comprises an important first step in identifying pre-European fire events in *E. regnans* forests to extend fire-climate analyses over century time-scales. However, significant advances on the current long-term dendro-climatological record – which is currently limited to long-term temperature reconstructions generated from *Lagarostrobos franklinii* tree rings (Cook *et al.*, 2006) - are required to elucidate fire activity with century-scale climate variation. Developing this area of research within *E. regnans* forests is of fundamental importance for contextualizing catastrophic fire events such as the February 2009 'Black Saturday' fire in Victoria that burnt over 450,000 ha - including vast areas of *E. regnans* forest – and for predicting the occurrence of stand-replacing fires under future climate scenarios (Lucas *et al.*, 2007).

A review by Keith *et al.* (2009) revealed that the amount of carbon storage in *E. regnans* forests is unparalleled throughout the world, with 13 old-growth stands (estimated to be > 250 years old) in the Central Highlands of Victoria containing an average of 1053 tonnes of carbon per hectare (tC ha⁻¹) in living aboveground biomass (Keith *et al.*, 2009). A single-cohort, old-growth *E. regnans*-rainforest stand in the Styx Valley some 6 km from our study

site was estimated to contain 850 tC ha⁻¹ in living above-ground biomass (Dean *et al.*, 2003; Dean and Roxburgh, 2006). Our data show that these forests not only store vast amounts of carbon, but also accumulate biomass quickly and maintain these high carbon densities for a long period of time (Figure 5.9). This is particularly important given the recent recognition that many old-growth forests up to 800 years of age continue to function as carbon sinks (Luyssaert *et al.*, 2008) and that wood production increases with tree size through old age in unsuppressed *E. regnans* trees (Sillett *et al.*, 2010). We suspect that *E. regnans* stands made up of old-growth eucalypts with a well developed rainforest understorey constitute a particularly carbon rich successional stage. However, there are few biomass data available for southern Tasmania to predict the carbon storage implications for these forests if the transition to rainforest occurs in the prolonged absence of disturbance or through conversion to regenerating forest by wildfire or harvesting.

Keith *et al.* (2009) argued that conserving forests with large stocks of biomass from deforestation and degradation, and restoration of a forests carbon sequestration potential should be among allowable mitigation activities under the United Nations Framework Convention on Climate Change. Estimates of both the magnitude and duration of maximum carbon storage discussed here provide useful upper bounds to which carbon storage of forests in various stages of successional in the landscape can be compared, and the carbon sequestration potential estimated (Smithwick *et al.*, 2002; Roxburgh *et al.*, 2006; Mackey *et al.*, 2008). This is best accomplished using landscape-level approaches such as the modelling studies of Dean *et al.* (2003; 2004) and Dean and Roxburgh (2006), who explicitly incorporate topographic and climatic variability and a range of fire and harvesting scenarios to forecast carbon sequestration in *E. regnans* systems. Ideally, such modelling would be underpinned by precise data on past fire events identified using dendrochronological techniques such as those developed here, but also account for potential changes in fire

regimes under future climate scenarios. The occurrence of extreme fire weather is predicted to increase in south eastern Australia (Lucas *et al.*, 2007) and subsequent increases in fire frequencies are likely to have a profound influence on fluxes and storage of carbon in forest systems prone to stand-replacing fire (i.e. Kasischke *et al.*, 1995; Kashian *et al.*, 2006). Consequently, management of these forests to maximise their carbon storage potential must not only focus on the effects of harvesting on carbon storage (e.g. Mackey *et al.*, 2008), but also consider the management of fire in the landscape (e.g. Hurteau *et al.*, 2008; Bradstock and Williams, 2009).

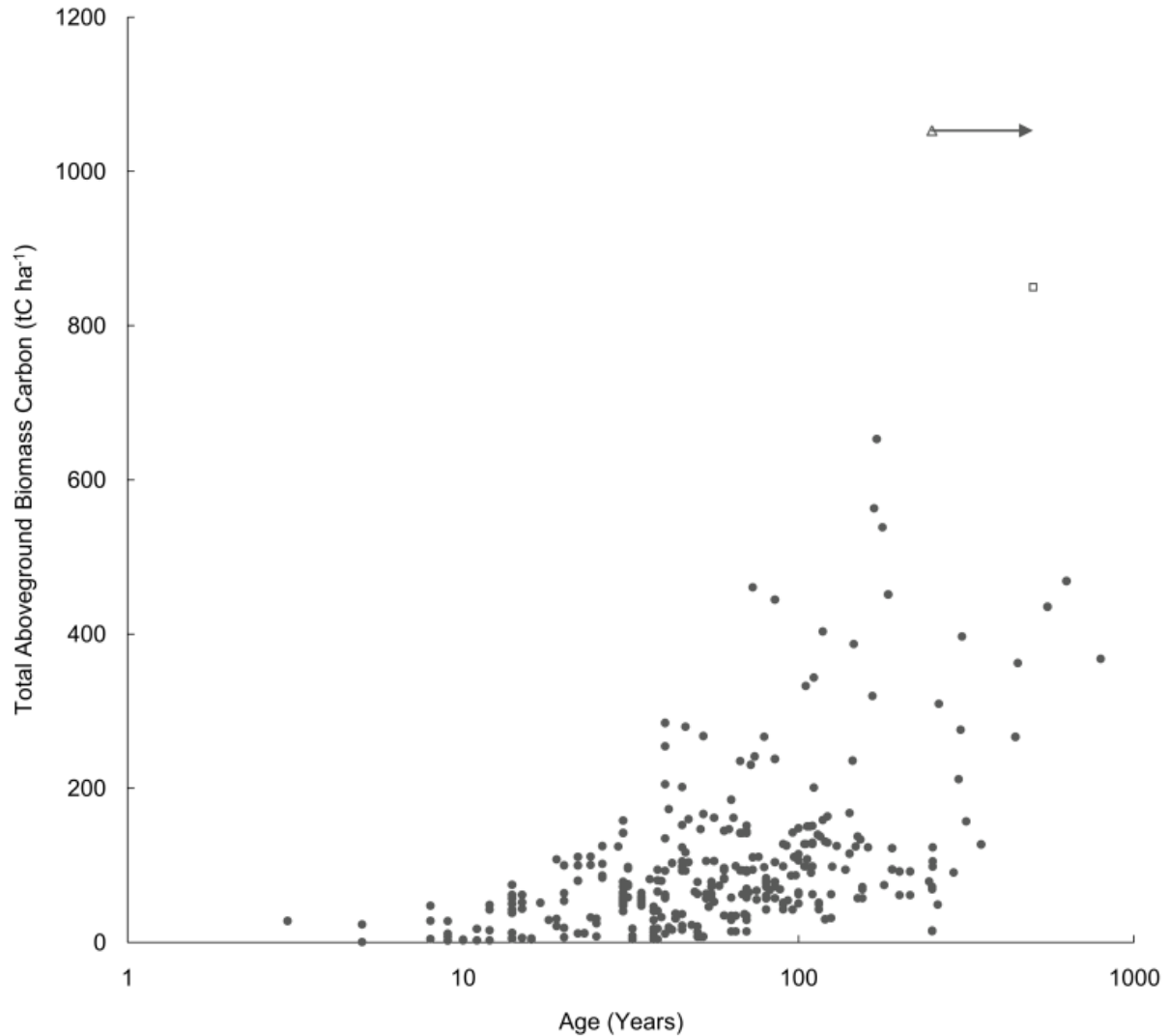


Figure 5.9. Carbon storage as a function of stand age for temperate forest ecosystems, shown as the relationship between aboveground biomass carbon (tonnes carbon per hectare: tC ha^{-1}) and the logarithm of stand age. Each data point represents a forest stand, many of which have different growing conditions and species composition. Closed circles represent temperate forests and are from the publically available database compiled by (Luyssaert *et al.*, 2007). The open square is for an *E. regnans* stand in the Styx Valley in Tasmania, with biomass carbon based on an old-growth *E. regnans* stand studied by Dean and Roxburgh (2006) and stand age based on dendrochronological data from this study. These two Styx Valley stands were only 6km apart (Figure 5.1b) and had a similar stand structure of low density, large diameter *E. regnans* trees over a rainforest understory. The open triangle is for the average biomass carbon for 13 *E. regnans* stands in the Central Highlands of Victoria, southeastern Australia, with the oldest cohorts assumed to be >250 years old (Keith *et al.*, 2009). Our data indicate that the oldest cohorts in the Victorian study may be over 500 years old (see arrow).

Chapter 6: Synthesis and Conclusions

Synthesis and Conclusions

The landscapes of southwest Tasmania are of high conservation value and form a large part of the Tasmanian Wilderness World Heritage Area. Many of the natural and cultural values that are central to the heritage status of this region are inextricably linked to the remarkable lowland (c. < 900m) vegetation mosaic of fire-sensitive and fire-adapted vegetation communities. The less productive parts of the southwest Tasmania include tracts of moderately flammable sclerophyll forest and fire-sensitive rainforest embedded in a matrix of highly flammable treeless moorlands. The more productive areas include stands of the tallest flowering plant on earth, *Eucalyptus regnans*.

Progress toward understanding how these vegetation patterns have evolved has led to the development of two models of vegetation dynamics (Figure 1.4). Jackson (1968) proposed the ‘edaphic drift’ model, which is effectively an alternative stable states model, whereby largely stable vegetation communities are maintained by feedback mechanisms between fire, vegetation and soil, but improbable changes in fire frequencies can result in vegetation transitions (Figure 1.4a). Similar models of alternative stable vegetation states have been proposed for other fire-mediated ecosystems (e.g. Warman and Moles, 2009; Staver *et al.*, 2011), many of which drew inspiration from the concepts inherent in Jackson’s model (Latham, 2003; Odion *et al.*, 2010). The Mount (1979) ‘stable fire cycles’ model is effectively a ‘sharpening switch’ model (*sensu* Wilson and Agnew, 1992), where vegetation patterns are largely determined by underlying physical environmental factors such as geology, soils, topography and drainage, and these relationships are ‘sharpened’ by very strong feedbacks between vegetation and fire to the point that vegetation transitions are impossible (Figure 1.4b).

The alternative stable states model of Jackson (1968) has garnered widespread support as the most suitable model for southwest Tasmania (reviewed by Bowman and Wood, 2009). However, the evidentiary basis for this widespread acceptance is lacking, particularly regarding the spatio-temporal resolution of field studies (Thomas *et al.*, 2010). The first aim of this thesis was to build upon previous historical ecology studies in southwest Tasmania by contributing new spatially explicit evidence on vegetation dynamics over decadal, century and millennial time scales. The second aim of this thesis was to investigate the role of interactions between fire, vegetation, soil and physical environmental variables in influencing the distribution and dynamics of southwest Tasmanian vegetation communities.

This chapter synthesises the key findings from this thesis with other ecological studies in the region (see Table 3.3) and discusses the implications for the Jackson (1968) and Mount (1979) models of vegetation dynamics for southwest Tasmania. Importantly, this thesis does not seek to resolve the debate between the two competing models. Instead the concepts and hypotheses inherent in the models are used as a framework for discussion.

Spatio-temporal vegetation dynamics in southwest Tasmania

Millennial scale vegetation dynamics in forest-moorland mosaics

Southwest Tasmania has one of the most comprehensive series of pollen and charcoal records in Australia and thus the millennial scale dynamics of broad vegetation communities throughout the Quaternary is very well documented. Recently, Fletcher and Thomas (2007a,b; 2010a,b) put forward a persuasive argument for a remarkable degree of stability in the distribution of rainforest and moorland vegetation types throughout the Holocene. They concluded that moorland has dominated the landscape since the Late Glacial period and that

fires ignited by humans are the primary agent responsible for this dominance (Fletcher and Thomas, 2010a). This work supersedes previous models of vegetation change that invoke the expanding and contracting of rainforest extent in southwest Tasmania throughout the Holocene (Macphail, 1979; Colhoun, 1996). Whilst these studies have provided invaluable insights into broad phytogeographical trends over millenia at regional scales, they cannot detect more localised shifts in vegetation boundaries. The analysis of stable carbon isotopes collected in well dated organic soil profiles is commonly used to examine long term vegetation boundary fluctuations (e.g. Bowman and Cook, 2002; Krull *et al.*, 2007). Unfortunately, this technique cannot be applied in southwest Tasmania because of the ubiquity of plants that use the C₃ photosynthetic pathway in all vegetation communities (Chapter 4). The analysis of pollen and charcoal trends from lake sediments and/or soil profiles strategically located on each side of a moorland-forest boundary may provide high spatial resolution data with a millennial perspective, but identifying suitable sites is problematic (Michael Fletcher, pers comm.).

Century scale transitions in mixed eucalypt-rainforests

Results from the dendro-ecology work conducted in this study (Chapter 5) in the mixed eucalypt-rainforests of southern Tasmania suggest that Gilbert (1959) and Jackson (1968) underestimated the time frame required for the transition from eucalypt forest to rainforest in highly productive sites. Based on their understanding of the longevity of the eucalypt dominants, Gilbert (1959) and Jackson (1968) suggested that transitions to rainforest following the loss of the eucalypts would take 350-450 years (Figure 1.3). However, in the carbon dense forests of the Styx Valley, where Gilbert and Jackson formulated their ideas, *Eucalyptus regnans* can live for well in excess of 500 years (Chapter 5). Clearly the rate of the transition to rainforest in these highly productive forests should be revised. Whether other

eucalypt overstorey species in less productive areas can live for this long is debatable and needs to be tested using the methods developed in this study.

The pioneering of high precision dendro-ecological techniques in Tasmania's southern forests has significant implications for future research into forest dynamics in Tasmania. There is now an opportunity to move beyond tree-ring counting and inferences of age based on diameter distributions to generate robust data on stand age structures and facilitate the precise dating of fire events. For example, stand age data derived from cross-dated tree ring chronologies are required to validate the diameter-age relationships that underpin the results of Turner *et al.* (2009) who found that single cohort forest stands are the exception rather than the rule in the wet forests of Tasmania. This is important because a predominance of multi-aged stands in the landscape implies a limited applicability of the proposed ecological models for large areas of forest in southern Tasmania. In this study (Chapter 5), a previously unknown fire event in ~1500AD was identified. How far did this particular fire spread? Can we identify other pre-European fire events? Answering these questions using dendro-ecology will help build on our understanding of the temporal and spatial pattern of fire in these forests.

Decadal scale vegetation dynamics in forest-moorland mosaics

The distribution of forest and non-forest vegetation across a representative southwest Tasmanian landscape has remained largely stable over the last 62 years (Chapter 3). This is consistent with the long-term maintenance of vegetation communities built into the models of both Jackson (1968) and Mount (1979). However, there were small fluctuations on forest boundaries at the decadal scale. Forest vegetation recovers quickly from single fire events that encroach across the forest boundary and forest expansion into treeless moorlands in the

absence of fire occurs in close proximity to the forest boundary and is exceedingly slow (Chapter 3). The slow rate of forest expansion observed in our study is supported by field evidence from the only other decadal scale study in the region (Brown *et al.*, 2002).

The observed boundary shifts lend support to the ‘ecological drift’ of vegetation boundaries proposed by Jackson (1968) although the rate of forest expansion appears to be far slower than Jackson implied. A strict interpretation of Jackson’s model predicts a shift from non-forest to forest across the landscape over 120-200 years in the absence of fire (Figure 1.3). King (2004) adjusted this for nutrient poor substrates to be 175-300 years. Assuming a constant rate of forest expansion of 5.6 hectares per decade, it would take approximately 2900 years for forest to replace the 1605 hectares of non-forest that existed in the Melaleuca Study Area in 2010 (calculated from data in Figure 3.3, Chapter 3). There are limitations to this ‘back of the envelope’ calculation. Is the rate of forest expansion constant over time? Does the expansion rate change as moorland gaps are infilled by forest? Is our 62 year analysis window long enough to detect change? Nevertheless, given the magnitude of the apparent disparity, it is likely that these limitations would not affect the conclusion that transitions from non-forest to forest are almost certainly much slower than the Jackson model suggests. Our findings are supported by recent simulation modelling of fire and vegetation dynamics in southwest Tasmania (King, 2004; King *et al.*, 2006; King *et al.*, 2008), where simulation results indicated that Jackson may have significantly underestimated the time taken for transitions between vegetation types.

Fire-vegetation-soil feedbacks and the role of physical environmental factors

Feedbacks between fire frequency and vegetation

Analysis of the spatial pattern of four very large wildfires in this study (Chapter 2) revealed that the flammability of southwest Tasmanian vegetation communities follows a distinct hierarchy: moorland > sclerophyll scrub > wet sclerophyll > rainforest. Whilst the exceptionally high flammability of moorlands is very well documented (Marsden-Smedley and Catchpole, 1995a,b,c) and there are some local data on the flammability of several forest types (see Pyrke and Marsden-Smedley, 2005 and references therein), this study provides the first integrated data on the relative flammability of four major vegetation communities at the landscape scale. The hierarchy of flammability across vegetation types matches the hierarchy of time-since-fire for these vegetation communities (Brown and Podger, 1982a). Collectively, these studies provide strong, yet inferential, evidence supporting the proposed fire frequency distributions that underpin the ecological models proposed for the region (Jackson, 1968; Mount, 1979).

The quantifying of actual vegetation specific fire frequencies central to the feedback mechanisms proposed for southwest Tasmania remains elusive. Estimates of fire frequency in long lived forest systems can be made using dendrochronological analysis of fire scars (Swetnam, 1993; Brown and Swetnam, 1994) or using data on the age structure of vegetation communities (van Wagner, 1978; Reed, 1994; McCarthy *et al.*, 2001). Indeed, Jackson apparently characterised fire frequencies using the ‘average age of a large numbers of samples of six main plant communities’, although details of the methods used were not documented. Quantifying stand ages for moorland and scrub communities could incorporate the preliminary work of Jarman *et al.* (1988b) and Marsden Smedley (1998). However, data

on stand ages of forest vegetation outside the highly productive wet eucalypt forests is extremely scarce (Harris *et al.*, 2009) and the dendrochronological potential of the dominant eucalypt of southwest Tasmania, *Eucalyptus nitida*, remains untested. Importantly, there are stands of *Athrotaxis selaginoides* within the region, which have the potential to yield high resolution data on fire events from well dated fire scars (Tom Veblen pers comm.) and tree ring chronologies (Allen *et al.*, 2011). Progress in these areas of research is crucial for appropriate testing of the Jackson (1968) and Mount (1979) models and represents a considerable – but essential – challenge for future studies in the region.

Feedbacks between fire frequency, vegetation and organic soils

It has now been clearly established that the chemical and physical characteristics of the organic soils of southwest Tasmania vary with vegetation type. This study showed that the physical properties of organic soils differ among vegetation types according to soil organic carbon, soil depth, the rate of organic matter accumulation, basal age and the degree of humification (Chapter 2 and Chapter 3). These findings broadly agree with those of the most comprehensive study of organic soils conducted in western Tasmania (di Folco, 2007). It is clear that forest vegetation has higher levels of phosphorus than non-forest vegetation at the landscape scale (Chapter 2) and this trend is related to a systematic increase in phosphorus from moorland, through scrub and eucalypt forest, to rainforest (Chapter 2 and Chapter 3; see also Bowman *et al.*, 1986). Importantly, these interactions are likely to be mediated by topography and its effect on drainage (Chapter 3; di Folco, 2007). These observations are consistent with Jackson's (1968, 2000) hypothesis that repeat fires deplete nutrient stocks in the organic soils of frequently burnt vegetation and that the absence of fire in forested vegetation allows net nutrient accumulation. However, it is still not possible to rule out the

effect of intrinsic differences in the fertility of the underlying substrate (i.e. Mount, 1979) in explaining these patterns.

The extent to which this disparity in nutrient stocks affects vegetation growth is important to interpreting the degree of resilience afforded by these fire-vegetation-soil feedbacks. It is likely that phosphorus has the potential to limit, but not entirely preclude tree growth in moorland vegetation in southwest Tasmania (Chapter 2 and Chapter 3; see also Read, 2001). Reciprocal transplant experiments (i.e. Maranon and Bartolome, 1993; Peltzer, 2001), where forest species are planted in moorland soil and vice versa, are an obvious pathway for future investigations into the influence of fire-vegetation-soil feedbacks in southwest Tasmania. The effects of added nutrients and different burning frequencies could be incorporated into these experiments.

Interactions between fire frequency, vegetation and topography

The analysis of the spatial distribution of rainforests and the spatial pattern of wildfire (Chapter 2) confirmed the previously untested assumption (Jackson, 1968; Mount, 1979) that topography exerts an overarching control on the fire-vegetation feedbacks that drive vegetation dynamics in southwest Tasmania. Fire occurrence in southwest Tasmania is clearly related to landscape position, with fire being more likely to burn on flats, ridges and steep north-facing slopes and less likely to burn in valleys and on steep south-facing slopes. Fire-sensitive rainforest preferentially occupies parts of the landscape where fire is least likely to burn (i.e. topographic fire refugia). Accordingly, the suite of fire-adapted communities in southwest Tasmania probably occupies parts of the landscape where fire is more likely to burn. The nature of these relationships could be readily tested using the modelling framework developed in this study (Chapter 2).

Interactions between fire frequency, vegetation and other physical environmental factors

The relationships between fire frequency, vegetation and other physical environmental variables such as geology and drainage remain unresolved. The statistically higher clay content of mineral soils under forests compared to non-forest vegetation (Chapter 3) implies an underlying geological control on vegetation distributions (i.e. Mount, 1979). However, even under forests, the levels of clay are extremely low and thus this observed difference in mineral soil texture may not be functionally important to plant growth. Balmer (1990) also found no evidence of significant transitions in geology or mineral soils across similar vegetation boundaries in southwest Tasmania. In eastern Tasmania, moorland-heath vegetation is clearly associated with parts of the landscape with impeded drainage (Jarman *et al.*, 1988a) and it is highly likely that seasonally waterlogged sites in southwest Tasmania favour the maintenance of moorland communities at the expense of forest communities (Pemberton, 1988; Brown and Podger, 1982a; Brown, 1999). The modelling framework developed in Chapter 2 could incorporate spatial data on geology and drainage to test the relationships between vegetation and drainage or geology at the landscape scale (e.g. Murphy *et al.*, 2010). At present, geology is available at the coarse resolution of 1:250,000 and attempts to model drainage using topographic features (i.e. topographic wetness index; Moore *et al.*, 1993) in this study produced very poor approximations of actual drainage patterns (Chapter 2, data not shown). Significant improvements in spatial data for these variables are required before adequate modelling exercises can be undertaken.

Vegetation dynamics in southwest Tasmania

Drawing on all available historical ecology evidence collected in southwest Tasmania (palynology, monitoring plots and repeat image analysis) reveals predominantly stable

vegetation communities at a range of temporal scales. This supports the concept of long-term resilience of vegetation communities inferred by both Jackson (1968) and Mount (1979). We observed localised transitions close to non-forest - forest boundaries at decadal to century scales. Accordingly, vegetation dynamics appear to conform to the alternative stable states model put forward by Jackson (1968) although the time frames for particular vegetation transitions appear to be significantly underestimated.

The resilience of each vegetation community is almost certainly related to the complex suite of feedbacks (Figure 1.4c) between fire and vegetation put forward by Jackson (1968) and Mount (1979). Remotely sensed observations of vegetation flammability and estimates of time-since-fire in vegetation communities support the concept of distinct fire frequencies inherent to each vegetation community. Observations of increasing phosphorus in organic soils across vegetation boundaries from moorland through eucalypt forest to rainforest support the concept of fire-vegetation-soil feedbacks (Jackson, 1968), although the role of underlying substrate fertility in explaining these patterns (Mount, 1979) remains unresolved. Interactions with topography add further resilience to the system. It seems that Jackson (1968) may not have fully appreciated the magnitude of resilience provided by this suite of feedbacks, hence the underestimation of the time frames for vegetation state transitions.

Demonstrating alternative stable states in terrestrial landscapes with long lived species is inherently difficult, with few studies able to meet all of the criteria required to unambiguously demonstrate vegetation stability or persistence (Petraitis and Latham, 1999; Beisner *et al.*, 2003; Schroder *et al.*, 2005). Southwest Tasmania is no exception and although we present robust evidence of the requisite state-transition vegetation dynamics and feedback mechanisms to support the Jackson alternative stable state model, our conclusions must remain equivocal. For example, the relative role of positive feedbacks (i.e. Jackson, 1968)

and physical environmental factors such as geology and drainage (i.e. Mount, 1979) in controlling vegetation distribution remains unresolved. Additionally, whilst there is strong evidence of the maintenance of particular vegetation communities at millennial (moorland and rainforest) and decadal (non-forest and forest) scales, we lack evidence of the maintenance (or lack thereof) of other vegetation communities (e.g. wet sclerophyll forest or mixed eucalypt-rainforest) at relevant spatio-temporal scales. Unfortunately, there are no current historical ecology approaches to rectify this situation. Nevertheless, the evidentiary basis for alternative stable states in southwest Tasmania is probably as comprehensive as most other studies that speculate fire-mediated alternative stable vegetation states in similar terrestrial landscapes (Petraitis and Latham, 1999; Perry and Enright, 2002; Latham, 2003; Hoffmann *et al.*, 2009; Warman and Moles, 2009; Odion *et al.*, 2010; Nicholas *et al.*, 2011).

That the vegetation communities of southwest Tasmania may represent a range of alternative stable states has important implications for the management of high conservation value rainforest vegetation under projected climate and fire regime scenarios. The predicted drier and warmer summers for the region (Grose *et al.*, 2010) are likely to lead to an increase in fire activity (Lucas *et al.*, 2007). Under such conditions rainforest vegetation relying on strong positive feedbacks for its maintenance become vulnerable to the so-called fire trap. Under the ‘fire trap’ scenario (Figure 6.1), feedbacks that maintain rainforest vegetation may be weakened by the drying out of currently wet and humid vegetation. Simultaneously, higher fire frequencies in flammable communities strengthen feedbacks between fire, vegetation and soil, thus increasing their resilience. Consequently, rapid transitions from rainforest to one of the more flammable communities become increasingly likely. These transitions are quickly reinforced by fire-vegetation-soil feedbacks, thus forcing a hysteresis in the system and creating a largely irreversible ‘fire trap’. An extreme example of this scenario is the complete removal of organic soils by fire (Bowman, 2007). The fire trap has

been proposed for a range of other fire-driven landscapes (Gignoux *et al.*, 2009; Hoffmann *et al.*, 2009; Odion *et al.*, 2010). Detecting the onset of such transitions and subsequently resorting these landscapes presents a considerable research and management challenge (Hobbs and Suding, 2008).

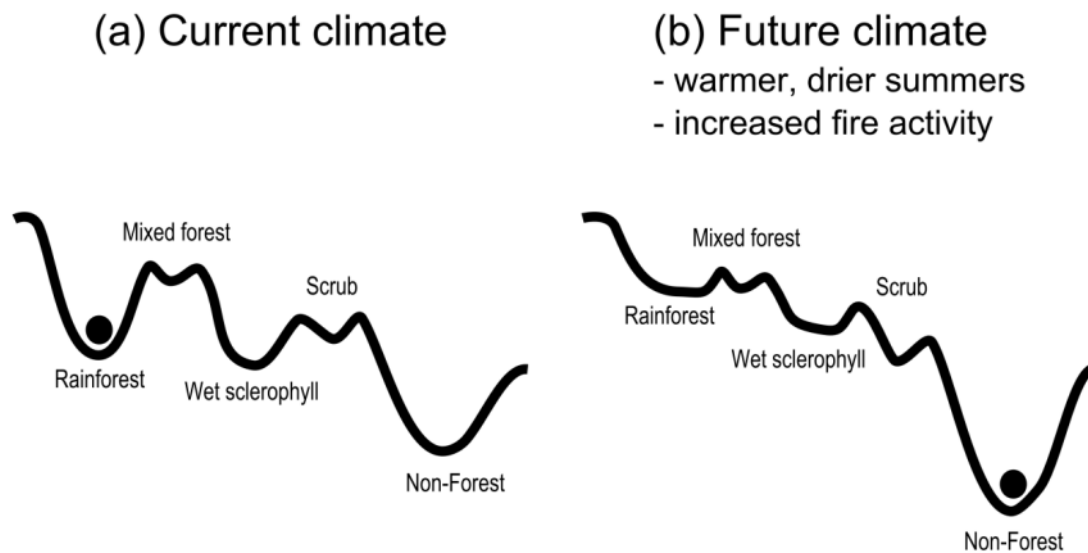


Figure 6.1. Alternative stable state scenario under (a) current and (b) future climates. Under the predicted warmer and drier summers in southwest Tasmania, feedbacks maintaining rainforest vegetation are weakened resulting in a shallow basin of attraction. Simultaneously, higher fire activity strengthens the feedbacks of highly flammable communities such as Non-Forest (i.e. moorlands) resulting in a deeper basin of attraction. The ball currently in rainforest is easily pushed beyond its resilience threshold and the reverse transitions are very unlikely resulting in a major hysteresis in the system, i.e. the fire trap.

As demonstrated by this thesis, southwest Tasmania is an ideal research laboratory to investigate how vegetation, humans, the physical environment, fire and climate have interacted to shape an iconic vegetation mosaic. Understanding the complex interrelationships between these factors is particularly pertinent in the face of anthropogenic climate change. Observing real-time shifts in vegetation and fire regimes now and into the future is crucial to future testing of models of vegetation dynamics. This points to the

establishment of a well designed monitoring system for the Tasmanian Wilderness World Heritage Area. A preliminary strategy for the implementation of such a system has been documented (Brown, 2010) and includes a combination of remote sensing, field monitoring and simulation modelling. The studies conducted in this thesis should be incorporated into this monitoring system. For example, future remote sensing should encapsulate the Melaleuca Study Area (Chapter 3) to capitalise on the time depth afforded by the repeat aerial imagery analysis. Mapping of wildfires using remote sensing (Chapter 2) is not currently employed by management agencies and should be implemented for timely and accurate delineation of fire boundaries. Finally, the relationships between fire, vegetation and the physical environment found in this thesis should be incorporated into simulation models that are currently used for planning of fire and vegetation management in the World Heritage Area (i.e. King *et al.*, 2006; 2008).

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Appendix 1:

The following list includes all peer reviewed papers that cite Jackson (1968) according to Google Scholar. The number of each reference refers to numbered circles in Figure 1.5.

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Appendix 2:

Correlograms of residuals of non-spatial (left-hand column) and spatial, autoregressive error (AR_{err}) models (right-hand column) of rainforest occurrence (a), and fire occurrence in moorland (b), sclerophyll scrub (c), wet sclerophyll (d) and rainforest (e).

